

Vol. 13, No. 2

November 1944

THE JOURNAL  
OF  
ANIMAL ECOLOGY

EDITED FOR THE  
BRITISH ECOLOGICAL SOCIETY

by  
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CAMBRIDGE UNIVERSITY PRESS  
LONDON: BENTLEY HOUSE  
BOMBAY, CALCUTTA, MADRAS: Macmillan

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*Single numbers: twenty shillings*

PRINTED IN GREAT BRITAIN

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## THE GRAZING OF WINTER CEREALS BY THE WOOD-MOUSE (*APODEMUS SYLVATICUS*)

BY A. ROEBUCK, F. T. BAKER AND J. H. WHITE, *Midland Agricultural College*

(With Plates 1 and 2)

### 1. INTRODUCTION

Extensive grazing of winter wheat over several years by an unknown pest, causing considerable damage in scattered localities throughout the whole of the Midland Province (Nottinghamshire, Lincolnshire, Derbyshire, Leicestershire and Rutland), led to a thorough investigation of the cause of the trouble. The grazing was remarkably regular and in many cases the whole of the field was systematically nibbled down and appeared quite brown, when ungrazed fields were green. It had been suggested that rabbits were responsible, but grazed fields in Derbyshire, where the rabbit (*Oryctolagus cuniculus*) was completely absent, showed the same damage and indicated that there was another explanation. Further, the grazing appeared too regular and systematic for the rabbit, which usually feeds in irregularly distributed patches. At Legsby, Lincolnshire, where this damage was very extensive, rabbits were remarkably scarce. Also, it was noticed that in all cases the damaged fields adjoined or were in close proximity to woods or spinneys, which suggested some association between the pest and these habitats. With these factors in mind the investigation commenced in 1941. The farm chosen for the experimental work was Bleasby House, Legsby, Lincolnshire, where Mr J. V. Dring had experienced trouble of this nature over the last 15 years and where it was always possible to forecast the fields adjoining a large woodland (250 acres) that would be liable to severe attack. Experimental work was undertaken in 1941, 1942 and 1943, and definitely established the pest as the wood-mouse (*Apodemus sylvaticus sylvaticus* (L.)).

### 2. NATURE OF DAMAGE

#### (a) Field characteristics

The most noticeable feature is the regularity of feeding. Beginning from the woodland or adjoining hedge colonized by *Apodemus*, the plants are eaten off and a well-defined line of attack is established. This, for convenience, is described as the 'feeding front'. In some cases where a field adjoins a wood, and a hedge at right angles to the wood is colonized, then two 'feeding fronts' are established at right angles. The 'feeding front' remains a constant field characteristic throughout the whole of the period of

attack, and wherever it was observed, trapping always indicated the predominance of *Apodemus* over other small rodents. Indeed, in 1943, out of 12 fields trapped on different farms to test this characteristic, only one field produced any other species in addition to *Apodemus*.

#### (b) Time and duration of attack

The attack usually develops within a week of the appearance of the plants above ground (Plate 1, photos. 1, 2), and proceeds systematically until the early months of the year, when growth of the plant tends to neutralize any further grazing that may take place. In the initial stages, when the plant is small, the attack progresses with great rapidity, and tends to slow down in December-January. This is quite natural, for as the plants become larger fewer will be required per mouse to make up the weight of food needed. This is only one factor, however, contributing to the slower rate of progress; trapping results (discussed later) indicate a reduction in the number of mice feeding during January.

After the initial establishment of the 'feeding front' the rate of progress of attack varies, but on field 1 at Legsby during the optimum period the front moved 5 yd. per night, which is equivalent to 0.3 acre. In 1942 damage began at Legsby on 14 Dec., 5 days after the first appearance of the wheat; on 17 Dec. a plot containing undamaged plants was marked out about 50 yd. from the wood. On 19 Dec. this plot showed 20% damage and by 22 Dec. 60% of the plants were affected. In one case in 1943 a 'feeding front' was established on a 14-acre field of winter wheat by 23 Oct. By 13 Nov. a third of this field had been eaten off, and by 29 Nov. approximately three-quarters of the field was grazed. Thus, in 5 weeks, *Apodemus* had completely grazed approximately 10 acres. This rate of progress was by no means abnormal, the attack in other fields under observation proceeding at a similar rate.

#### (c) Type of grazing

*Apodemus* attacks the cereals at all stages from the first appearance of the plant above ground. Shortly after the appearance of the plant the leading shoot and first leaves are taken off as though grazed. The grazing is not close to the ground, but a portion of the stem of varying height is left showing above

ground. The part of the plant left has a clean-cut edge and nowhere are ragged edges found. The leaves which subsequently unfold show this same characteristic (see Plate 2, photo. 3). Where the plant is in a more advanced stage of development the leaves are nipped off towards the base, again leaving a clean-cut edge. Leaves up to 4 in. in length are nipped off leaving about  $\frac{1}{2}$  in. near the base. Comparison made between plants attacked by *Apodemus* and those known to have been eaten by rabbits, show that the latter have a more ragged edge and the length of leaf left is much more variable—from 2 in. to none at all (Plate 2, photo. 4). Differentiation between the attacks of the two animals may be made by an examination of the individual plants (Plate 2, photos. 5, 6).

(d) *Plants damaged*

Attacks have been noted and confirmed on winter wheat, winter oats, rye and winter barley. Where a choice between winter wheat and winter oats or barley is provided, there is a preference for wheat. In 1935 at the Midland Agricultural College this mouse was responsible for the destruction of crocus corms and carnation cuttings.

(e) *Economic importance of damage*

In severe cases the attack by *Apodemus* has been known to cause complete failure. In 1942 at Legsby a field of winter wheat was so badly affected that there was no alternative but to plough it in. Where the attack is less severe and the plants recover sufficiently to avoid ploughing in, there is always a considerable reduction in weight of grain per acre and the date of harvesting is delayed. In Mr Dring's long experience of this pest the reduction on such fields amounts to from 2 to 2½ qr. per acre, and the quality of the grain is very poor owing to the late development of the plant after this setback. Harvesting is delayed. In the case of other smaller farmers whose land adjoins the Bleasby Woodland, the War Agricultural Executive Committee has modified the demands for wheat acreage owing to the limited choice of fields where winter wheat can be grown without risk of attack by *Apodemus*.

### 3. IDENTIFICATION OF THE PEST

(a) *Preliminary investigations, 1941-2*

In 1941 two fields south and west of Bleasby Wood were extensively damaged. The field west of the wood was almost completely grazed. Adjoining this field farther to the west, another field of winter wheat, drilled at the same time, was almost free of damage. These two fields were divided by a ditch containing several inches of water. This appeared to be a natural barrier preventing the creature responsible for the damage from obtaining access to the field farther from the wood. It was therefore suggested that the damage was probably caused by a mammal moving

from the wood, since the latter was not enclosed by wire-netting and the surrounding ditch was quite dry.

In 1942 the following experimental plots (5 × 5 ft.) were laid down on 25 Nov. shortly after the wheat had been drilled:

(1) *Metaldehyde*. A heavy dressing was scattered over the surface of the ground. This had no effect in controlling the damage to the wheat. No slugs were found. The previous crop of potatoes had been free from slug damage.

(2) *Balloon silica*. This was dusted over the ground at frequent intervals as a precaution against frost damage. This was also quite ineffective.

(3) *Paris green and bran*. A heavy dressing was applied. It was noticed that some measure of control was effected at first, but the plot showed considerable damage after 10 days as the effectiveness of the poison bait diminished. No dead animals were found.

(4) *Plots protected by netting*. (a) *Complete protection*.  $\frac{1}{2}$  in. wire-netting was used. An enclosure was made 5 × 5 × 2 ft. The netting at the sides was buried 6 in. The top was covered over by lengths of the same material. (b) *Partial protection*. As above, but the top was left open.

In neither case was there any damage inside the enclosure, while the grazing was complete right up to the wire-netting of both plots.

The evidence of these experimental plots further pointed to a mammal as the cause of the attack. It was, therefore, decided to put down traps in order to determine the animal responsible, which was thought to be a nocturnal feeder. Spring break-back traps were set about the field and baited with cheese. The first traps were put down on 23 Dec., but trapping had to be discontinued owing to hard frosts and snow. Traps were again put in the field in January 1943 and by 20 Jan. the following results were obtained:

Species	No. trapped
<i>Apodemus sylvaticus</i> (L.)	23
<i>Microtus agrestis hirtus</i> (Bellamy)	5
<i>Sorex</i> sp.	5

Thus, of the herbivorous species, *A. sylvaticus* numbered 82% and *M. hirtus* 18%.

These observations led to the conclusion that the grazing was most probably due to *Apodemus*, which is known to feed upon the leaves and stems of plants. An examination of the wood revealed that the mice were living in the dike banks and deep burrows in the roots of trees and shrubs. One nest was found 10 yd. in the field from the wood. The nest was in use and *A. sylvaticus* was trapped at the entrance to the burrow.

(b) *Further investigations, 1943*

Trapping in 1943, carried out in many fields over the whole Province, confirmed *Apodemus* as the cause of the damage. Twelve fields were specially investigated, eleven of which have given by trapping only



Photo. 2. Heavily damaged young wheat, 31 January 1944.  
Field 1, Bleasby House, Legsby.

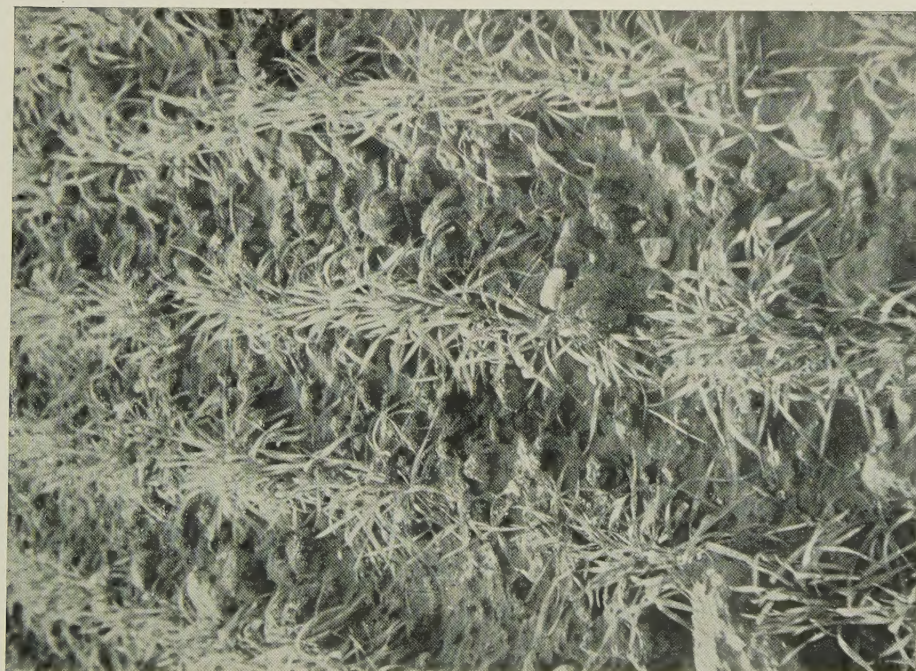


Photo. 1. Undamaged young wheat, 31 January 1944.  
Field 1, Bleasby House, Legsby.

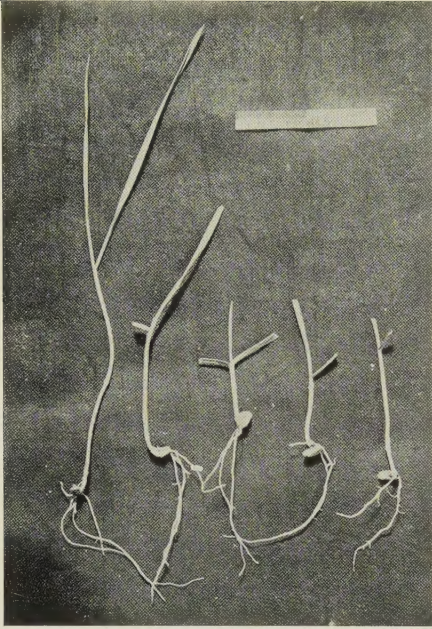


Photo. 3. Wheat plants attacked by *Apodemus sylvaticus*.  
Note clean-cut edge and regular character of grazing.



Photo. 4. Wheat plants (natural size) eaten off by rabbits. Note ragged edges and irregular grazing of plants.

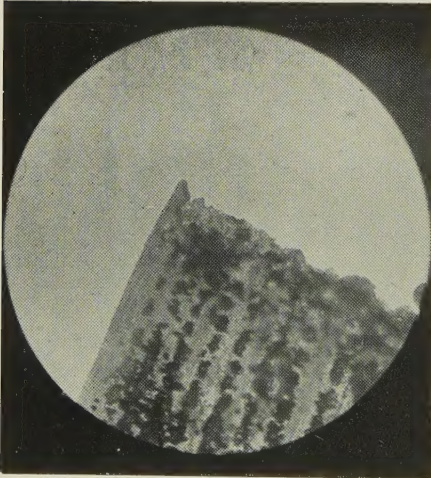


Photo. 5. Leaf of wheat eaten by *Apodemus sylvaticus*.

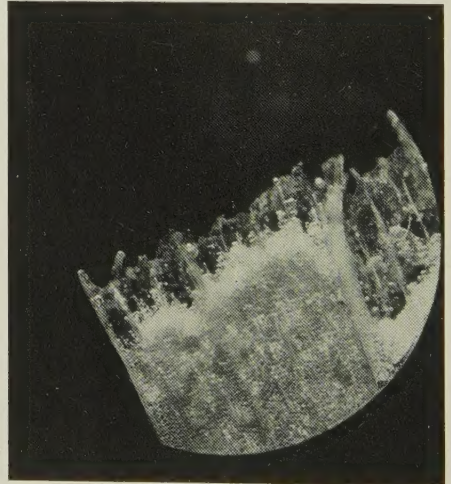


Photo. 6. Leaf of wheat eaten by rabbit.

*Apodemus* (the other gave one *Microtus*). At Bleasby House, Legsby, where intensive trapping was carried out on two fields, 168 *Apodemus* were captured and no other species taken.

**Trapping technique.** Trapping was carried out by means of live traps in place of the unsatisfactory break-back. The trap used was the Tring trap (see Chitty, 1937). The trap was provided with a nest-box containing dried material and food. By this means the mice were captured alive and could be released, where necessary, after examination. The traps were baited with cheese.

**Trapping on field 2.** Twenty traps were placed in the field on 25 Nov. These were arranged in pairs—five pairs in each of two groups—ten close to the wood (the main source of the mice) and

great disparity between the sexes, the male is more active and on the whole ranges farther afield. This corroborates work by Chitty (1937) and Evans (1942). The greatest range noted by us was 165 yd. from the nearest hedge.

#### 4. INDOOR OBSERVATIONS ON DAMAGE

Five *Apodemus* were retained indoors for observation. They were fed on ground oats. After a time trays of germinated wheat were introduced and the reactions of the mice noted. Their first action was to begin burrowing in the soil, which appeared to be the greatest attraction. Later, they were observed eating the germinated grains thus disturbed. An examination of the trays after a night's activity revealed

Table 1. *Trapping results in field 2*

		Traps (field numbers)																				
		Near the wood										Near the 'feeding front'										
Date		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
26 Nov.		—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3
27		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	2
29		1	1	—	—	2	—	—	—	1	1	1	1	1	—	—	—	—	1	—	1	11
30		—	—	—	—	—	—	—	—	1	1	1	1	—	1	1	1	1	1	1	1	11
1 Dec.		1	1	—	—	—	—	—	—	—	1	—	1	—	1	—	—	1	—	—	—	6
2		1	1	—	—	1	—	—	—	—	1	1	1	—	1	1	—	—	—	1	1	10
3		1	—	—	—	1	—	—	—	—	—	—	1	1	—	1	—	—	1	1	1	8
4		1	—	—	—	—	1	—	—	—	1	1	1	1	1	—	—	1	1	1	1	11
6		1	—	—	—	1	—	—	—	—	1	1	—	1	—	—	—	1	1	—	—	7
7		—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	1	—	—	—	4
8		—	—	1	—	—	1	—	1	1	1	—	1	—	—	—	1	1	1	—	—	9
9		1	—	—	—	—	1	—	—	—	1	1	1	1	1	—	—	1	1	—	1	10
10		1	—	—	—	1	—	1	—	—	—	—	—	1	1	—	—	1	1	—	1	8
14		—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	1	—	3
15		—	—	—	—	1	—	—	—	—	1	1	—	—	—	—	—	—	1	—	—	4
16		—	—	—	—	—	—	1	—	—	—	1	1	—	1	—	—	—	—	—	1	5
17		Traps closed until after poisoning																				
Total		8	3	1	1	7	5	2	1	4	9	9	10	7	8	3	2	8	10	5	9	112

ten just behind the 'feeding front'. The traps were examined at almost daily intervals until 16 Dec. The mice captured were sexed and released and the traps reset. Any dead mice were collected and weighed. During the whole of this period only *Apodemus sylvaticus* was taken in the traps; no other small rodents were captured.

The following deductions can be drawn from these trapping results:

(1) The large number of mice (71) caught in the traps behind the 'feeding front' compared with the smaller number (41) in the traps on the grazed area nearer the wood, indicates that the majority of mice move straight out to the feeding area and do not remain to feed on the area already attacked. In view of this, further trapping was concentrated upon the 'feeding front'.

(2) Of the mice sexed, there were 58 males and 25 females. It seems, therefore, that unless there is

numbers of plants nipped off in the same way as observed in the field, though the whole effect was spoilt by the extensive burrowing and consequent uprooting of the plants. Close observation in the field, where *Apodemus* was known to be present in numbers, to check up on this apparent habit of disturbing the plant and eating the grain, failed to produce a single comparable example. This was apparently the result of the mice being confined under unnatural conditions where opportunity for natural burrowing was not provided.

#### 5. OTHER OBSERVATIONS ON *APODEMUS SYLVATICUS*

**Habitat.** *Apodemus sylvaticus* colonizes the woodland, hedge-banks and dike-banks that have direct communication with the wood. In the hedge and dike-banks the colonies decrease in numbers farther

from the wood. Only very rarely have holes been found out in the field. Entrances to burrows were noted well inside the wood. It has not been possible to determine the full extent of penetration, but it is known to exceed 20 yd.

*Nesting.* The main nesting sites are deep in the roots of trees and shrubs, with extensive, winding burrows leading to them. Occasional nests have been found in the field. The nests are round, about 6 in. in diameter and 3 in. inside and composed of dry grasses and dead leaves. No winter stores have been located.

*Feeding.* Experiments carried out indoors with mice fed on ground oats gave the average nightly consumption of food as about 5 g. per mouse. Although no strict comparison may be made between dry and green food material and the requirements of captured and free mice, it is of interest to note that 42 plants (average length of leaf material 4 in. per plant) weigh 5 g. It may, therefore, be deduced that in the initial stages of the attack, when but  $\frac{1}{2}$  in. of plant is available, the number of plants eaten per mouse per night may be more than twenty times the figure given above.

## 6. CONTROL

### (a) *Poison bait*

To determine a suitable bait for poisoning, trays each containing about 65 g. of the following substances were placed in the field and covered from above to prevent birds taking the bait:

- (a) Sausage rusk—dry and moist.
- (b) Crushed oats—dry and moist.
- (c) Meal (mixed cereal and linseed)—dry and moist.

These substances were placed in separate trays and three groups of six trays were distributed about the field. In all cases it was found by inspection that more *dry, crushed oats* had been taken than any other base. This was repeated with the same results. It was, therefore, decided to use dry, crushed oats as the base for poisoning.

The method of prebaiting as used so successfully by the Oxford University Bureau of Animal Population (Chitty, 1942; Morgan, Fisher & Watson, 1943; Ministry of Food, 1944) was adopted from the commencement. On field 1, twelve prebaiting points were put down on 27 Nov.—some on the 'feeding front' and others distributed over the field. Each point consisted of a tray of dry, crushed oats, covered with a larger inverted wooden tray propped up at one corner or an inverted wooden box with semicircular holes to allow entry of mice. These prebaiting points were examined daily and the trays filled up with crushed oats. The amount consumed by the mice was noticed to increase for a day or two and then remain fairly stable at about 30 g., leaving a surplus. This conclusion was based on visual inspection,

without weighing; this applies also to observations that follow. The prebaiting points were not filled up after 2 Dec. and on 6 Dec. the poisoned bait was substituted in fresh trays. This consisted of a mixture of dry, crushed oats and zinc phosphide—the latter constituting 4% by weight of the mixture. On the following day it was seen that all the baiting points but one had been visited and the poisoned mixture taken. The poison bait was left until 9 Dec., but visits on 8 and 9 Dec. showed no more poison taken. The amount taken on the first night of poisoning was approximately 15–20 g., and on the next two nights together only about 3–4 g. Consequently, the baiting points were removed and eight traps placed in the field. The traps were visited on 10, 13, 14, 15 and 16 Dec. and no mice were captured. (On field 2 from 10 to 16 Dec., 20 mice were caught in 20 traps.) On 20 Dec. the traps were again visited on field 1 and two mice found. On 21st, there were none; 23rd, one; 24th, none; 26th, none; 28th, none; 29th, two; and 30th, two. On each occasion the mice were killed and the traps reset. Over this period, 29 Nov.–30 Dec., there was no appreciable movement of the 'feeding front'.

As it appeared from the trapping that the population was again building up, the prebaiting points were put down again on 30 Dec. and the traps removed. On this occasion, all the prebaiting points were placed on or about the 'feeding front', as it appeared from trapping evidence that this was the most suitable situation. These were visited on 31 Dec. and 3 Jan., and it was noted that mice had fed at all except one, but the amount of bait consumed was small compared with the first prebaiting. The poison mixture was put down on 5 Jan. and examination on 7 Jan. showed that only three points had been visited and a small amount of poison taken. Traps were put down and visited frequently, but no mice were taken until 21 Jan.

The same procedure was adopted on field 2. After prebaiting, the poison mixture was put down on 21 Dec., followed by traps. On 24, 26 and 27 Dec. no mice were captured. On 29 and 30 Dec. two mice were taken and on 31st, one. On 3 Jan. eight mice were trapped; on 5 Jan., two; 7 Jan. three. The traps were removed and prebaiting points substituted, but it was not until 24 Jan. that sufficient bait was being consumed to justify poisoning. No mice were taken in the traps put down after poisoning until the middle of February.

The reduction in the numbers trapped between 23 and 31 Dec., bears no relationship to the average minimum ground temperature over this period (23.6°F.). Over a similar period (26 Nov.–4 Dec.) with a similar average minimum ground temperature (24.5°F.), 62 mice were trapped.

*Conclusions.* Poison-baiting by this method does temporarily reduce the population of *Apodemus* feeding on the field and checks the attack. Where the

attacked field adjoins a large acreage of woodland (e.g. Legsby, 250 acres) local population fluctuations due to migration and immigration (cf. Evans, 1942) cause a further build-up of *Apodemus* near to the field and the attack on the wheat is resumed. The time taken for this adjustment of population to take place appears to be 2–3 weeks. Consequently, poison baiting by this method must be repeated frequently and its success is limited and depends on the area of woodland colonized by *Apodemus* and acting as a source of supply.

Every effort was made to trace dead animals in the field following the poisoning, but not one was recovered. Indoor experiments with the same pre-baiting and poisoning with 4% zinc phosphide bait gave a 100% kill on the first night of poisoning.

#### (b) Other notes on control

(1) It was demonstrated in preliminary work in 1941 that a deep ditch with running water provides a satisfactory natural barrier to *Apodemus*. This is not always practicable, but where a ditch occurs between a woodland and the field affected, deepening and widening is of value if it normally carries water as early as October–November.

(2) Gassing appears to be quite impracticable owing to the large number of holes and burrows in the hedge-banks, dike-sides and extending deep into the wood.

(3) There may be some relationship between the attacks by *Apodemus* and the systematic destruction of natural predators. At Legsby, there has been intensive game-keeping and Mr Dring states that he sees an owl, kestrel, stoat or weasel very rarely. On one occasion when a weasel (*Mustela nivalis* L.) was observed it was carrying a dead *Apodemus* in its mouth. The encouragement of natural predators may help in establishing a balance.

### 7. SUMMARY

1. *Apodemus sylvaticus sylvaticus* (L.) is responsible for extensive attacks on winter-sown cereals

throughout the Midland Province (Nottinghamshire, Lincolnshire, Derbyshire, Leicestershire and Rutland).

2. The characteristic damage is a systematic grazing of the young plants during the autumn and early winter. The plants are grazed to within half an inch of the ground.

3. A well-defined 'feeding front' or line of demarcation between the grazed and ungrazed parts of the field, is a constant field characteristic. This 'front' is pushed forward as the attack proceeds.

4. After severe attacks, especially if accompanied by bad weather, crops have to be ploughed up and spring crops sown.

5. On crops which recover the attack produces a loss of grain amounting to approximately 2–2½ quarters per acre and the quality of the grain is inferior. Harvesting is delayed.

6. Prebaiting, followed by poison-baiting with dry crushed oats and 4% zinc phosphide by weight, checks the attack. Local fluctuations in population due to migration and immigration make it necessary to repeat the prebaiting and poisoning at intervals of a fortnight.

### 8. ACKNOWLEDGEMENTS

The writers are much indebted to Mr Charles Elton and the staff of the Oxford University Bureau of Animal Population who placed at their disposal the whole of their work and wide experience on rodent control. Without this most valuable assistance the present work could not have been completed in so short a time. In addition, the Bureau very kindly loaned Tring traps for the field work. We are grateful also to Mr J. V. Dring of Bleasby House, Legsby, for the excellent facilities he has given to develop the work and for his constant encouragement and co-operation during the past 3 years. We are also indebted to Mr F. V. Mills for the excellent photographs illustrating this paper.

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# THE LIFE HISTORY AND GROWTH OF THE BROOK LAMPREY (*LAMPETRA PLANERI*)

By M. W. HARDISTY

(With 6 Figures in the Text)

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### 1. INTRODUCTION

In view of the complete absence of information as to the duration of the larval period of the brook lamprey, *Lampetra planeri* (Bloch), in the British Isles, the present work was planned to obtain information on the growth of the ammocoete.

The area included in this study covered about 40 sq. miles in south-east Somerset, with the village of Bruton as the centre. Most of the streams are tributaries of the River Brue which rises some 4 miles east of Bruton. Collections of larvae and adults from streams in this area were made during 1938 and 1939, and further larvae were taken from the River Yeo in north-west Somerset in 1940.

The work was undertaken in the Department of Zoology of the University of Bristol under the direction of Prof. C. M. Yonge, whose constant advice and encouragement I wish gratefully to acknowledge. My thanks are also due to Mr J. Z. Young, of the Department of Zoology and Comparative Anatomy, Oxford University, whose generous help at the outset made this study possible. I should like to thank the many people, particularly my wife, who have assisted in the collection of larvae.

### 2. LIFE HISTORY AND HABITS

#### A. Adults

##### (1) Spawning grounds

The positions of spawning grounds which have been discovered are shown on the map (Fig. 1). It is safe to assume that many other places where adults have been seen are close to spawning sites.

At seven localities spawning was observed in exactly the same position during 1938 and 1939, and in one instance for the three previous years also. In

many cases the nests were situated either directly under a bridge or only a short distance below, suggesting that shade was a factor involved in the selection of the spawning site. Adults in confinement show the same preference for shade. Where the spawning grounds were not under a bridge, the position was usually partly shaded by trees or buildings.

In six cases the nests occurred just below a weir or rapids over which it would have been difficult for the lampreys to pass. Although the bed of the stream at the spawning ground was often composed of sand or gravel, in some cases it consisted of stones and small boulders, and spawning has even been observed on a surface of bare rock.

The depth of water over the nests never exceeded 18 in. and was usually not more than 10 in., irrespective of the size of the stream above and below the spawning ground. Where nests were placed just below a stretch of deeper water, it was observed that none extended into it, although the character of the stream in other respects remained uniform throughout. This preference for shallow water may be connected with the poor visual apparatus of the lamprey making orientation in deep water difficult. The nests were not found where the current was swiftest, but just above rapids where the deeper and calmer water began to break up. In every case they were either in a depression, or behind or in front of some obstruction such as stones or driftwood. Observation showed that, although the current above the nest might be too strong for the animals to withstand, when not anchored by the sucker, there existed in the nest itself a 'pocket' of quiet water. Reighard (14) believed that the existence of such pockets determined the spawning location, but as many exist in stretches of the stream where spawning does not take place it

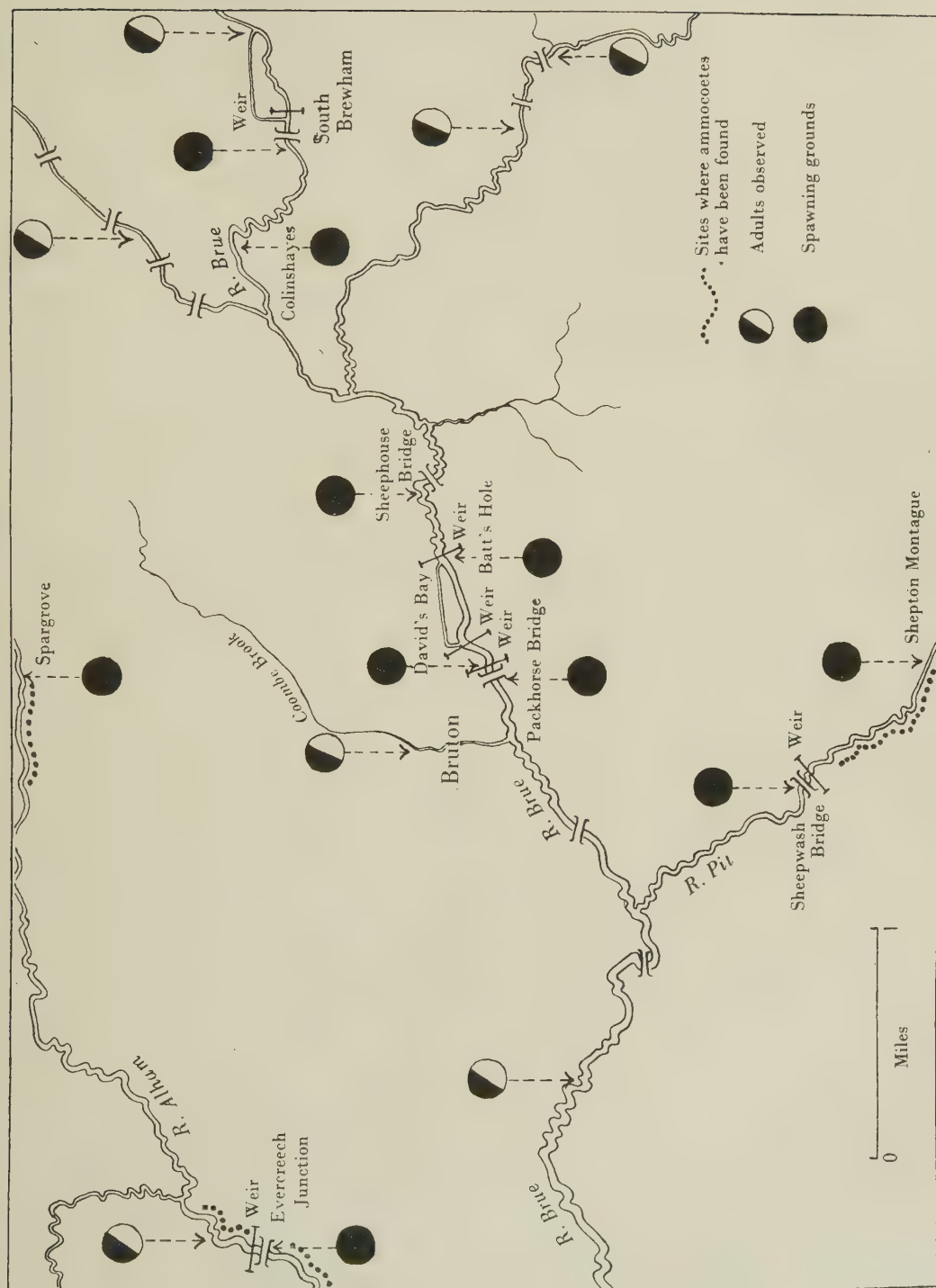


Fig. 1. Map of the area covered by the present study, showing the position of the spawning grounds.

cannot be the only factor involved. In many cases the decisive factor was the presence of weirs or low waterfalls which bring the upstream spawning migration to a halt. Thus in the River Brue near Bruton there were three such spawning grounds within less than a mile, each placed just below a weir and therefore drawing its spawning population from only the limited stretch of stream between two weirs. These adjacent populations are only isolated from their

isolated or grouped closely together. Where close, the occupants have been observed to wander from one nest to another, confirming the conclusion of Reighard(14) that there is no constant relation between individual fish and individual nests.

Table 1. Records of water temperatures (°C.) during the spring of 1939

Date	R. Brue		R. Alham	R. Pit
	South Brewham	Bruton	Ever- creech Junction	Shepton Montague
5 Feb.	6.1	—	—	—
12	7.2	—	—	—
18	—	—	7.4	8.0
19	7.2	—	—	—
27	5.8	—	—	—
5 Mar.	8.5	—	—	—
6	—	8.0	—	—
7	—	—	8.0	7.6
11	—	—	8.8	8.6
12	6.4	6.7	—	—
13	—	—	—	—
18	—	6.7	5.5	7.2
20	5.8	—	—	—
26	—	5.4	5.0	5.0
28	4.7	—	—	—
1 Apr.	—	7.6	8.2	7.8
3	8.3	—	—	8.3
5	8.8	9.2	—	—
6	—	7.8	8.3	8.0
8	8.8	—	—	—
9	10.8	8.0	—	—
10	11.0	9.6	10.8	11.9
11	10.3	11.0	—	11.9
12	10.0	11.7	—	—
13	8.8	11.2	—	—
14	—	10.7	—	10.7
15	—	11.0	10.1	10.0
16	11.0	10.5	—	—
17	11.0	10.4	10.3	—
18	—	—	10.6	—
19	—	10.6	—	—
20	11.2	—	—	—
21	—	12.2	—	—
22	12.2	—	—	10.7
24	11.9	—	—	8.8
26	8.8	—	—	—
28	8.8	—	—	—
29	—	—	—	—

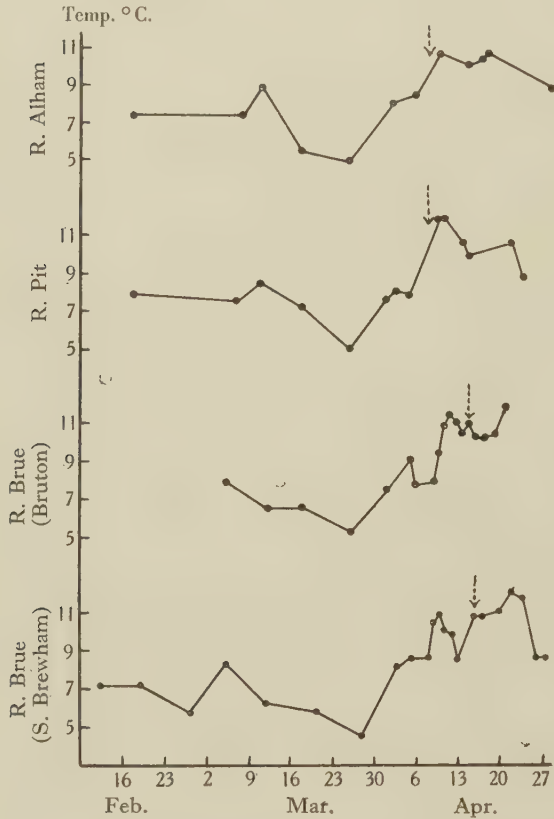


Fig. 2. Water temperatures of the Brue, Pit and Alham rivers during February, March and April 1939. The commencement of spawning is indicated by the arrow.

downstream neighbours, and will receive ammocoetes from farther upstream, especially during periods of flooding.

The character of the nests varied with the nature of the bottom. Where this consisted of gravel or sand it took the form of a circular or oval depression from 1 to 4 in. deep, and from 6 to 18 in. in diameter, according to the number of animals it contained. At the downstream end there was often a low heap of small pebbles and gravel which had been dislodged by the vibratory activity accompanying spawning or carried out of the nest by the animals. In stony places there was little or no depression and the heap of pebbles was often absent. The nests were either

(2) Spawning temperature

In 1938 spawning dates varied considerably at the different spawning grounds and it was thought that differences in temperature might account for this. During 1939 records were kept of water temperature at four stations and the results are given in Fig. 2 and Table 1. These results do not account for the differences observed in 1938.

The variable and unstable weather conditions of spring 1939 make the determination of the spawning temperature difficult. During March, temperatures fell below February levels and there was considerable

rainfall. Heavy flooding occurred in the first week of April and this was immediately followed by a period of warm sunny weather, causing a sharp rise in water temperature. Fully mature animals were caught as early as 21 March, although none were seen in the nests until 9 April. On 1 April and again on the 3rd specimens were found in spawning condition, and indeed two females had in all probability actually spawned, yet at no time had the temperature risen above 8°C.

On 3 and 4 April there was heavy rain causing severe flooding. By 11 April following several days of warm sunny weather, lampreys were spawning in the River Pit and River Alham with water temperatures of 11.0 and 11.5°C. respectively. Spawning lasted a few days only and the last specimen was found in the River Alham at Evercreech Junction on 18 April.

In the River Brue spawning reached its peak somewhat later (15 April), but continued for a longer period during which temperatures varied from 11.0 to 12.0°C.

Evidence has already been given that spawning may have taken place in some cases at temperatures below 8.0°C. and it would certainly appear to be possible long before the earliest date when it was observed. Specimens caught on 22 March and placed in a tank exhibited spawning activities, such as stone carrying and vibratory activity, within 3 days, and eggs and sperms were easily expressed, resulting in fertilization.

On 12 April 1940 spawning was observed at many points in the River Yeo near Wrington (Somerset) at a water temperature of 10.0°C. It is suggested that the spawning temperature in Somerset lies between 10.0 and 11.0°C., but when delayed by adverse conditions, such as flooding, spawning may occur at a lower temperature, while with a rapid rise in temperature it may occur at a higher figure.

Dean & Sumner(2) describe the spawning of the North American brook lamprey, *Entosphenus appendix*, at a temperature of 66°F. (18.9°C.) and Young & Cole(18) observed the same species spawning at 63°F. (17.2°C.). Schultze(15) suggested a critical temperature of 51–52°F. (10.5–11°C.) for *Lampetra planeri* in Michigan.

The adult emerges from the mud in early spring. In both 1938 and 1939 the first specimen was recorded on 11 March. These, together with those found during the following week, were caught under stones a short distance below the spawning grounds. They possessed none of the characteristics of sexually mature animals; the fins were slightly separated, with no swellings and the anal papilla of the male was not visible externally. When placed in a tank they invariably burrowed quickly underneath the mud. This burrowing movement seems to be confined to the sexually immature animals and has never been observed in lampreys taken from the nest.

Surface(16), Young & Cole(18) and others have stated that the male lamprey precedes the female to the spawning grounds and begins nest building first. Records kept of all captures failed to confirm this.

Collection of adult lampreys was made by hand-net, usually whilst they were together in the nests. When disturbed they lose their attachment by the sucker and drift downstream. The net is placed just below the nest and the animals are swept into it. None were obtained by dredging the mud, but a few were found under stones near the spawning places, or caught whilst swimming upstream towards the nests.

Animals taken from the nest and placed in a tank almost immediately engaged in stone carrying and vibratory movements. Having anchored with the sucker, the branchial region is raised sharply and the rest of the body is bent sharply downwards, whilst the tail vibrates violently. If a hold has been secured on a small enough stone, this would be raised and carried for a short distance. In this way small pebbles are carried down and across the stream, but only rarely against the direction of the current. Seldom are stones carried more than about 8 in. and they appeared to be dropped in a casual way, whilst the animal was still swimming. Having failed to raise a stone it did not persist, but wandered off and fastened on to another.

Although they are incapable of swimming with stones of greater diameter than about  $\frac{3}{4}$  in., larger stones may be moved by being pushed or dragged along for a short distance. By the wriggling and vibratory movements of the spawning mass, embedded pebbles are loosened and carried away together with the sand by the current.

It is certain from the great frequency with which mating takes place that both sexes must mate many times. The number of the two sexes in the specimens collected was nearly equal; out of 268 adults, 139 were males and 129 females.

After spawning the animals become sluggish and are often found under stones some distance below the spawning grounds. Spent specimens have never been found in the nests.

There was considerable variation in the size of the adults from different streams and even from different parts of the same stream. Thus for one spawning ground on the River Brue the average was 128.5 mm.  $\pm 1.74$ ; at South Brewham Bridge on the same stream 149.4  $\pm 0.71$ ; and for the River Pit 160.0  $\pm 2.18$ . There was also a considerable difference in the average length of the adults collected during the 2 years 1938 and 1939. For 1938 the average length of 114 specimens was 138.75  $\pm 2.19$ , and for 154 specimens in 1939, 147.5  $\pm 1.88$  (Table 2 and Fig. 3).

#### B. Larvae

The ammocoetes appeared to be generally distributed over the whole area, except in the upper courses

of the smaller streams. They are only to be expected where the current is sluggish or where the stream follows a meandering course. They were often found in eddies or backwaters below obstructions such as

Table 2. Frequency of adults collected during 1938 and 1939 arranged in length groups of 5 mm.

Length group in mm.	1938		1939	
	Males	Females	Males	Females
106-	—	—	—	1
111-	1	2	1	—
116-	3	1	1	—
121-	6	6	2	1
126-	4	2	4	1
131-	6	9	8	5
136-	11	9	9	3
141-	12	9	14	14
146-	7	11	12	20
151-	4	7	11	8
156-	—	1	13	5
161-	2	—	5	6
166-	—	—	2	4
171-	—	1	—	2
176-	—	—	—	—
181-	—	—	1	—
186-	—	—	—	1
Total	56	58	83	71

organic material. Where the deposit was shallow, they sometimes occurred in a mixture of silt and fine sand, but were seldom found in coarse sand or gravel. As both Maskell (11) for the New Zealand *Geotria australis*, and Schultze (15) for *Lampetra planeri* have remarked, they are most numerous toward the water-line and this may be due to the fact that there is usually a greater proportion of organic material in the upper part of the bank.

Schultze (15) found that his larvae were not segregated according to age; but in Somerset there were indications that the older larvae were more frequent in certain habitats. At one point on the River Pit where the deposit was fine silt, nearly 300 specimens were obtained, not one of which could with certainty be assigned to the oldest age group; while in a collection farther downstream where there was a deep layer of decaying debris there was a very high proportion of ammocoetes more than 2 years old. The same uneven distribution was also noted in the River Alham. The largest ammocoetes and metamorphosing specimens were usually found amongst debris containing little or no mud. Metamorphosing individuals were sometimes found in pure sand and even gravel. Table 3 gives a comparison of the composition of collections from different parts of the

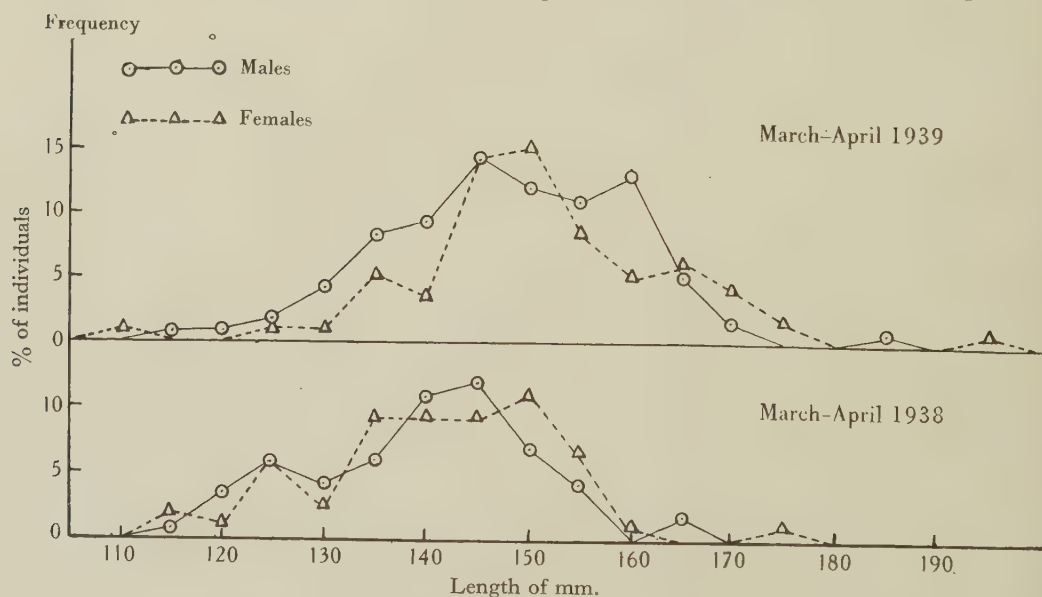


Fig. 3. Frequency curves for adults collected in March and April 1938 and 1939.

fallen trees and projecting roots, or on bends in the stream. At such places there were usually accumulations of silt covered by a layer of decaying leaves, sticks and debris. Although the type of mud inhabited by the larva varied, the deposit in which they were most numerous consisted of fine silt blackened by decaying organic matter, and the densest populations were associated with a high proportion of such

same stream (River Alham). Site A was some 3 miles upstream from site B and was situated in a bank of fine silt at a bend in the stream. Site B was an eddy off the main course of the stream and the deposit was silt overlaid by leaves and twigs. Both collections were made in September 1939.

The disparity is most marked in the much higher proportion of the smallest specimens at site A. This

sample shows the normal gradual decrease in the frequency of larger specimens, but site B has an increase in the third size group and a very much higher percentage of larger ammocoetes.

There was also a marked difference in the composition of collections from the small stream (River Pit) and the larger River Alham. This is illustrated by Table 4, which compares the September 1939 collection from the Alham with collections made in the Pit during August, September and October 1938.

Table 3

Size group mm.	Site A		Site B	
	No. of specimens	Percentage	No. of specimens	Percentage
0-	80	67.8	81	39.1
46-	25	21.2	35	16.8
76-	9	7.6	51	24.6
100-	4	3.4	23	11.1
Over 125	—	—	17	8.2

Table 4

Size group mm.	R. Pit		R. Alham	
	No. of specimens	Percentage	No. of specimens	Percentage
46-	213	76.3	63	27.4
76-	43	15.4	98	42.6
101-	19	6.8	42	18.2
Over 125	4	1.4	27	11.7

The size composition of the Pit sample resembles that of site A in Table 3. The evidence of partial segregation may be summarized thus:

(1) A high proportion of older larvae was usually found where there was an accumulation of vegetable debris.

(2) Samples from higher reaches of the stream contained a smaller number of the larger larvae than samples from downstream.

(3) The small stream (Pit) contained fewer older specimens than the larger River Alham.

It is probable that there is a gradual movement of the ammocoetes downstream resulting in a higher proportion of older larvae in the lower reaches, but this is almost certainly a passive migration during periods of flooding.

Eddies and backwaters would not be so affected by flooding, consequently the larvae which were carried into such places would tend to remain and the proportion of larger larvae would be greater than in places where flooding constantly removes some of the population. As it is in such protected places that masses of debris collect, it may be understood why a high proportion of larger larvae is usually associated with such accumulations. Apart from passive transportation the fact that the animals may be attracted

to rotting vegetation, as described by Enequist(3), makes it possible that they may make active movements for short distances towards areas of richer food material. Indeed, the same author asserts that the ammocoetes do not remain buried in the mud but adopt a free swimming mode of life at night.

Metamorphosis probably begins in July and continues until early winter. The earliest transforming specimen was found on 16 July. Others were found later in July and in August and September. No adult lampreys were ever found with the larvae.

### 3. GROWTH AND THE DURATION OF THE LARVAL STAGE

Müller(12) and Lubosch(10) gave estimates of 3 years for the larval stage. Loman(9) grouped his ammocoetes in four yearly classes and Hubbs(4), working on a Californian brook lamprey indistinguishable from *L. planeri*, suggested the same period. Larger collections have been studied by Schultze(15) in Michigan, and Ivanova-Berg(5) in the region of the Gulf of Finland. The former decided that spawning probably took place at the end of the fourth year, but was doubtful if age and rate of growth could be accurately traced by means of frequency curves right up to metamorphosis. Ivanova-Berg suggested a larval period of 4½ years and a total life span of 5 years. For the North American brook lampreys *Entosphenus appendix* and *Ichthyomyzon unicolor*, Okkelberg(13) gave estimates of 5 and 7 years respectively for the total life span. Knowles(8) followed the progress of a group of the larger ammocoetes (80 mm. upwards) from April to December in collections from the River Sarno near Naples, finding that these spawned the following spring. The total life span was estimated as not less than 3 and not more than 4 years.

Collections were made monthly in the River Pit from May 1938 to April 1939, with the exception of January when heavy flooding made this impossible. A stout iron ring fitted with a net of strong fine mesh curtain material was used to dredge out the mud, which was tipped out on to the bank and sorted. The larvae were measured alive with calipers the same day, after being narcotized with urethane.

The stretch of the stream from which the ammocoetes were obtained extended for about three-quarters of a mile, bounded below by a weir preventing upstream movement of adults. The spawning ground from which the larvae are believed to originate lay about 1¼ miles upstream from the weir and no spawning was observed above this point.

Further collections were made in the River Alham during July 1938 and September 1939, and also in the River Yeo near Wrington in May 1940. The River Alham material was grouped in three lots, each consisting of ammocoetes drawn from the same part of the stream at about the same time.

The results of all these collections are given in Tables 5 and 6 and the corresponding frequency curves in Figs. 4 and 5. For convenience in grouping the histograms, the absolute frequency of each length group was used in the River Pit series, but in the case of the data for River Yeo and River Alham percentage frequencies were employed. While the evidence from these frequency curves cannot be considered conclusive, the interpretation to be advanced is believed to be the one that best accords with the data, and to assist in following this hypothesis the suggested age groupings have been indicated in the histograms.

after hatching these larvae grow to a length of about 30 mm. and in the following spring measure 30-40 mm. when 1 year old.

The further progress of this class during their second summer may be traced in the monthly series of the River Pit. The group as a whole moves forward during the summer of 1938 reaching a peak value of 60-65 mm. by October. They apparently recede during the winter, but go forward again in March and April 1939. In the April histogram these ammocoetes form a compact group from 45 to 85 mm. agreeing closely in dispersion with the second group

Table 5. Frequency of ammocoetes collected in the River Pit during 1938 and 1939, arranged in length groups of 5 mm.

Length group in mm.	1938									1939		
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		Feb.	Mar.	Apr.
26-	—	—	—	—	—	—	—	—	—	—	1	—
31-	1	—	—	—	—	—	—	—	—	1	2	—
36-	13	2	—	1	1	—	—	2	—	—	5	1
41-	22	7	4	1	2	2	2	6	4	9	—	—
46-	15	20	16	12	6	6	3	15	9	12	1	—
51-	4	18	18	16	16	11	6	26	14	13	11	—
56-	7	10	23	11	20	10	5	19	4	20	9	—
61-	6	2	13	14	13	16	13	14	6	12	10	—
66-	11	9	8	9	12	10	6	15	4	12	8	—
71-	5	7	14	12	15	4	4	5	4	7	10	—
76-	3	9	13	4	8	4	5	2	2	10	6	—
81-	3	2	6	4	4	7	3	—	1	3	3	—
86-	—	1	4	3	4	2	2	—	1	4	—	—
91-	—	—	4	2	—	3	4	—	1	1	1	—
96-	—	—	3	1	1	1	—	—	—	5	1	—
101-	1	—	3	1	1	2	—	—	1	1	1	—
106-	—	1	6	1	—	—	1	—	—	—	—	—
111-	—	—	3	2	—	—	1	—	—	3	2	—
116-	1	1	1	2	3	—	—	—	—	1	1	—
121-	—	—	—	4	—	2	—	—	—	—	1	—
126-	1	—	3	1	2	—	—	1	—	—	—	—
131-	—	—	—	—	—	—	—	1	—	2	1	—
136-	—	—	3	—	—	—	—	—	—	—	—	—
141-	—	—	1	—	—	—	—	—	—	3	—	—
146-	—	—	1	—	—	—	—	—	—	—	—	—
151-	—	—	1	—	—	—	—	—	—	—	—	—
156-	—	—	1	—	—	1	—	—	—	—	—	—
161-	—	—	—	—	1	—	—	—	—	—	—	—
Total	93	89	149	101	109	81	55	106	52	126	67	—

The May 1938 curve for the River Pit shows two peaks at 40-45 and 60-70 mm. respectively. There are further isolated specimens from 100 to 130 mm. The first class are taken to be in their second summer, since spawning did not take place until April. This is confirmed by finding a group of the recently hatched ammocoetes in the July 1938 material from the River Alham. These specimens which averaged 15-20 mm. were found shortly after severe flooding entangled in filamentous algae near mid-stream and some 100 yd. below the spawning grounds at Evercrech Junction. In the histogram of 8 Sept. these measure 20-25 mm., and in the curve of 23 and 30 Sept. they are grouped around a peak at 25-30 mm. During the first summer

in May 1938. This class, now 2 years old, shows some progression in the River Pit series as far as July, but from then onwards it is difficult to trace, although the October material suggests a second group with a peak of 80-85 mm. The disappearance of this class as a well-defined group in the later histograms may be connected with the downstream migration to which reference has already been made.

The River Alham material, containing a greater proportion of the larger ammocoetes, shows, in all cases, groups which can be identified with the 2-year-old class of the River Pit. Thus the July collection, in addition to the newly hatched and 1-year-old classes, has a third peak at 80-85 mm. The histogram

for 8 Sept. does not show compact classes, but there are ammocoetes from 40 to 75 and 80 to 115 mm. which apparently represent the 1- and 2-year-old groups. This collection, containing only a small percentage of larger specimens was made some 2-3 miles upstream from the sites of the remaining River Alham collections. The ammocoetes drawn from the same pool on 23 and 30 Sept. are grouped in four well-defined classes, the third of which, ranges from

Table 6. *Frequency of ammocoetes collected in the River Alham and River Yeo in length groups of 5 mm.*

Length group in mm.	R. Alham				R. Yeo
	July	8 Sept.	14 and 15 Sept.	23 and 30 Sept.	1940 12 May
16-	6	4	—	—	—
21-	12	28	3	2	—
26-	4	38	15	8	7
31-	—	9	47	20	21
36-	—	—	16	15	14
41-	—	1	—	8	9
46-	3	3	—	—	7
51-	15	10	2	1	11
56-	13	3	2	1	15
61-	15	—	15	6	14
66-	5	8	8	7	6
71-	4	1	8	13	8
76-	4	—	9	15	11
81-	7	1	14	12	11
86-	3	4	10	1	5
91-	2	1	13	7	6
96-	3	3	4	12	3
101-	3	—	5	6	3
106-	—	2	8	3	3
111-	1	2	5	4	3
116-	2	—	3	4	2
121-	1	—	2	2	—
126-	—	—	4	—	—
131-	—	—	3	1	—
136-	—	—	4	2	1
141-	—	—	1	2	2
146-	—	—	3	3	1
151-	—	—	1	2	1
156-	—	—	—	—	—
161-	—	—	—	—	1
166-	1	—	—	—	—
171-	—	—	—	—	—
176-	—	—	1	—	—
Total	104	118	206	157	166

90 to 125 mm. with a peak at 95-100 mm. and undoubtedly represents the 2-year-old ammocoetes. The collection of the 14th and 15th was obtained over a greater stretch of the stream and is therefore less homogeneous. This shows a second group from 50 to 95 mm. and a further peak at 105-110 mm. The evidence on the fate of these 2-year-old larvae, although less conclusive than in the case of the younger groups, suggests progress from 65-70 mm. in May to around 100 mm. in September, with a dispersion from 90 to 130 mm. Since the adult

lengths range from 110 to 190 mm. with an average of about 140 mm. (considerably higher than this in the River Pit), it is clear that few, if any, of this group would be sufficiently grown to metamorphose during their third summer, especially as allowance must be made for shrinkage in length between metamorphosis and sexual maturity (*vide infra*). This view is supported by the presence of a third group in the River Yeo in May from 70 to 120 mm. with a peak at about 80 mm. Similarly the April 1938 material for the River Pit has ammocoetes from 90 to 135 mm. beyond the preceding 2-year-old class.

The larger ammocoetes from 100 to 165 mm. found in the River Pit during 1938 must be at least 3 years old and some at least are large enough to transform, although very few metamorphosing specimens were collected and of these none was less than 135 mm. in length. The histogram for 23 and 30 Sept. (River Alham) has a fourth group from 130 to 155 mm.; that for 14 and 15 Sept. has ammocoetes up to 160 mm. apparently outside the range of the 2-year-old group. From both these collections only four metamorphosing ammocoetes were obtained.

In the River Yeo there appears to be a fourth group present in May from 140 to 175 mm. If valid, this would imply that some at least of the 3-year-old ammocoetes fail to metamorphose until the following year, which would explain the small proportion of transforming individuals found among this class in the autumn.

Thus while the data are not sufficiently complete to follow the progress of the older larvae in detail beyond the third summer, consideration of such factors as the relation of larvae and adult lengths make it probable that metamorphosis takes place at the close of the fourth summer or during the fifth. At metamorphosis the ammocoetes would be  $3\frac{1}{2}$ - $4\frac{1}{2}$  years old, and the adults 4 and 5 years old at spawning. Growth rates appeared to vary considerably in different streams. The average length of the larvae in the humps of the frequency curves was taken as an approximation to the average length of a yearly class. Comparing material collected during July 1938 the lengths of the well-defined 1- and 2-year-old classes was considerably greater in the River Alham compared with the River Pit (Table 7). Corresponding groups in the River Yeo are smaller than in the River Pit in May (Table 8).

Even within the same stream there was marked variation and it was noticed that in places where the bulk of the population consisted of younger classes, the average lengths of these groups tended to be less than in sites where a higher proportion of older ammocoetes was present. Owing to the continual downstream migration the older larvae would tend to accumulate in the lower reaches, in eddies or backwaters where greater deposits of organic material will provide a richer food medium and result in more rapid growth.

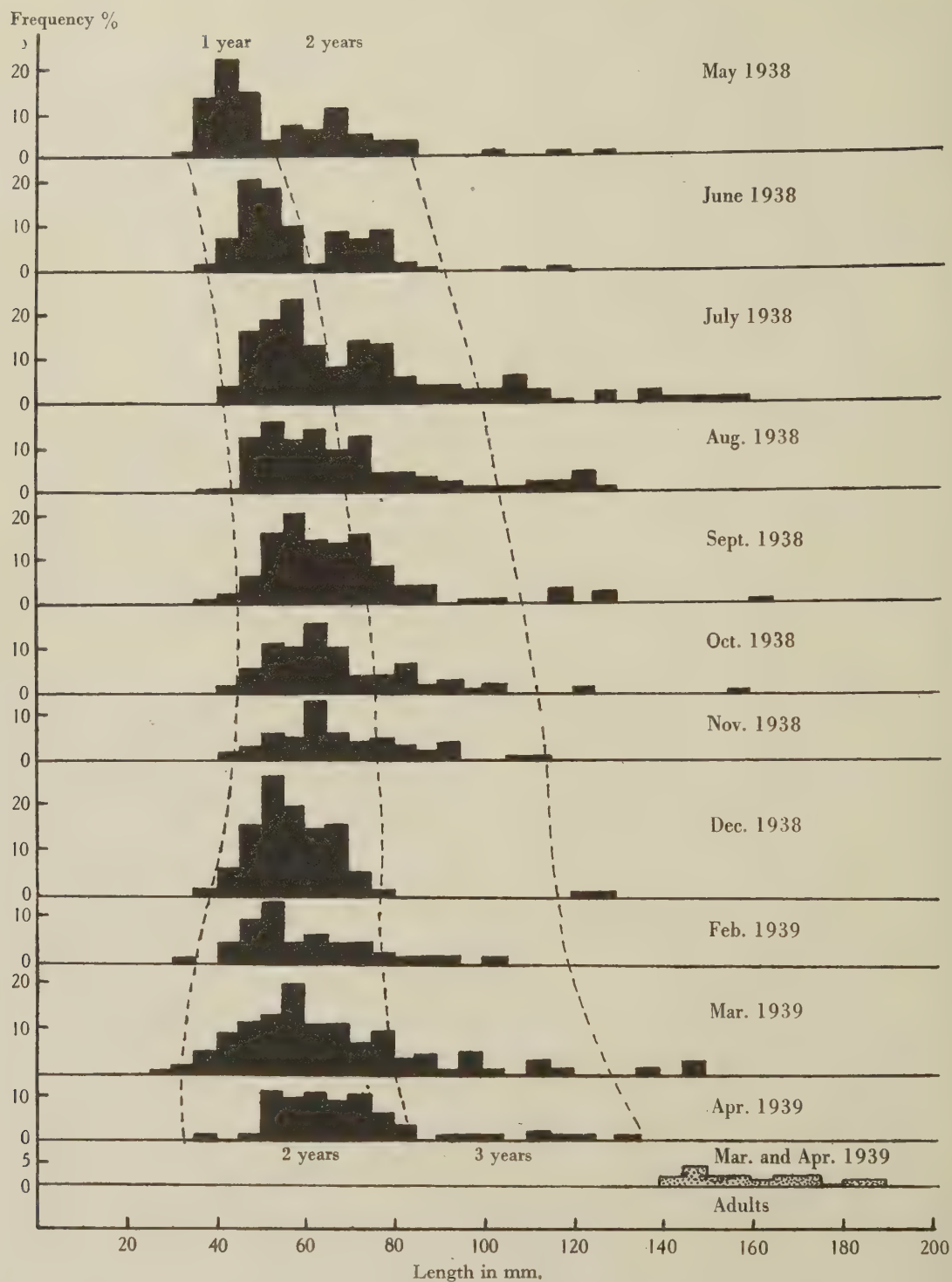


Fig. 4. Frequency curves for monthly collections of larvae from the River Pit, 1938-9.

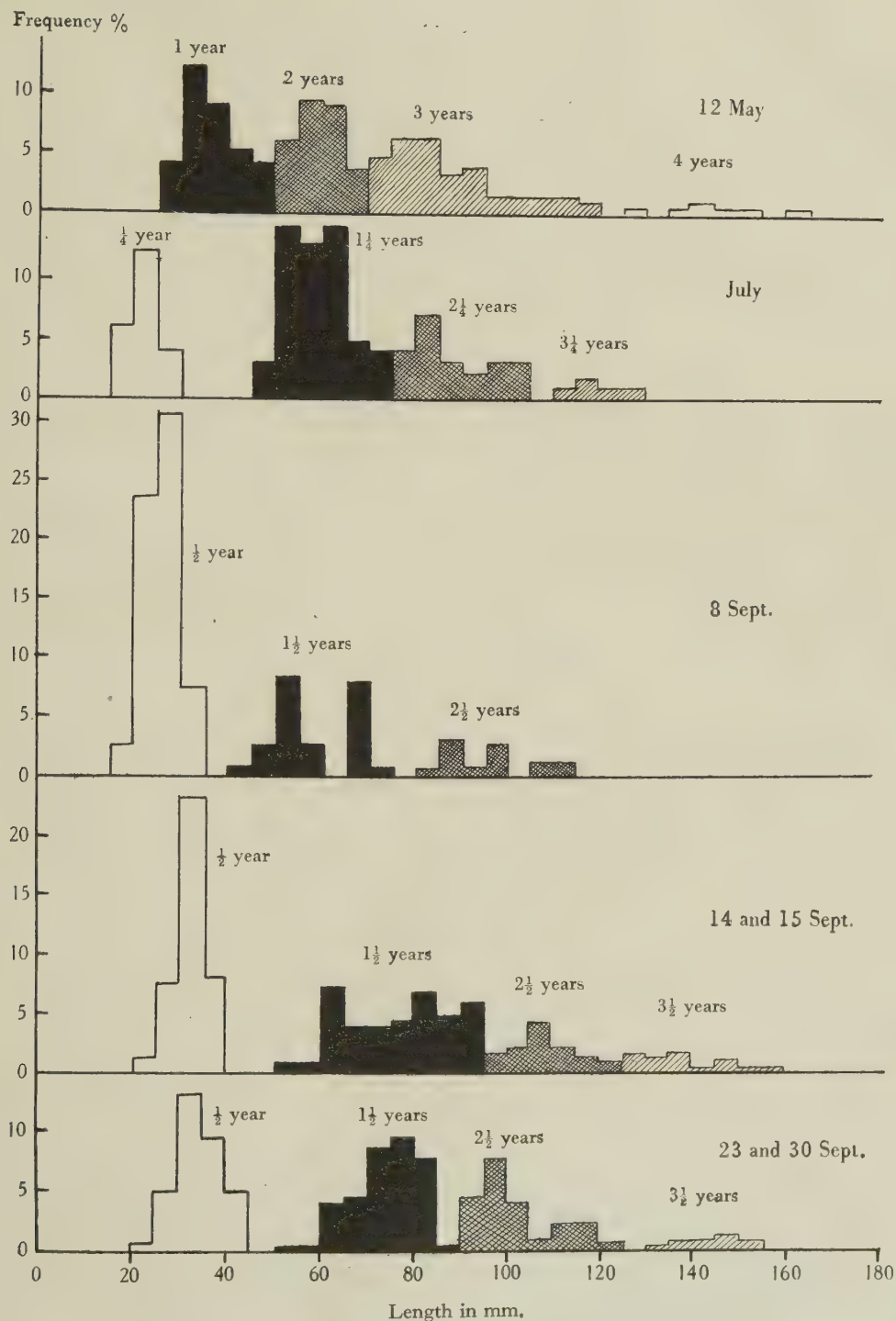


Fig. 5. Frequency curves for collections of larvae from the River Alham and River Yeo.

In spite of such local variations, Tables 7 and 8 show general agreement in the rate of growth over the first 2 years. So that a complete series could be obtained, the average length of the age groups was calculated from the clear-cut frequency curve for 23 and 30 Sept. (Table 9). These results were consistent with the available data for the River Pit and River Yeo. The question as to whether the 3½-year group fail to transform until the following summer cannot materially affect the result since they have already reached lengths similar to those of the adults from the same stream.

Up to 1½ years the growth rate is rising; between 1½ and 2 years it falls off, increasing again towards metamorphosis. There can be no further growth

Weight-length relationship

921 larvae and 154 adults were weighed, after drying between filter papers. The data were grouped in length classes of 10 mm. (Tables 10 and 11). When log-weight was plotted against log-length the curve could be divided into three sections, for each of which the points fell close to a straight line. Applying the formula  $W = cL^n$ , suggested by Keys(7) for the weight-length relation of fishes, the values of  $n$  for the three sections of the larval curve were:

Length (mm.)	Value of $n$
0-75	2.6
75-120	2.9
Over 120	3.7

Table 7

Age group yr.	Average length (mm.)	
	R. Pit 30 July	R. Alham 16 July
1½	55	59
2½	77	84

Table 8

Age group yr.	Average length (mm.)	
	R. Yeo 12 May	R. Pit 30 May
1	37	44
2	59	70

Table 9. 23 and 30 Sept. River Alham

Age group yr.	Average length mm.	Increment mm.	Percentage increment (of adult length)
½	34	34	23.5
1½	76	42	29.0
2½	104	28	19.3
3½	145	41	28.2
Adults	145	—	—

after transformation since, as Weissenberg(17) and Keibel(6) have established, the fore-gut becomes a closed tube.

Ivanova-Berg(5) found that, although growth was most rapid during the first 2 years and was then retarded, there was no acceleration in the final year. Sigmoid growth curves have been recorded by Hubbs(4) for the North American brook lamprey *Entosphenus appendix*, and by Okkelberg(13) for *Ichthyomyzon unicolor*. Knowles(8) found that his ammocoetes grew from 85 mm. to an adult length of about 120 mm. in their final year. He considered that the group measuring 85 mm. in April was not more than 2 years old, but this seems uncertain, bearing in mind the results obtained here (cf. River Yeo, Fig. 5) and the fact that spawning is much later in the River Sarno, i.e. May or June.

Table 10. Weight and weight-length coefficients for 921 larvae. In length groups of 10 mm.

Length group mm.	Fre- quency	Average length mm.	Average weight g.	$W/L_3 \times$ 10,000
21-	28	27.6	0.042	200
31-	55	34.8	0.085	202
41-	80	46.7	0.170	166
51-	190	55.3	0.259	153
61-	182	65.3	0.408	146
71-	134	75.0	0.583	138
81-	81	84.5	0.825	137
91-	59	95.3	1.165	135
101-	32	105.1	1.525	131
111-	33	115.4	1.946	126
121-	18	124.4	2.460	122
131-	13	135.0	3.186	129
141-	12	145.9	4.261	137
151-	3	153.7	5.215	144
171-	1	176.0	8.400	154

Table 11. Weight and weight-length coefficients for 154 adults. In length groups of 10 mm.

Length group mm.	Fre- quency	Average length mm.	Average weight g.	$W/L_3 \times$ 10,000
106-	2	111.7	2.447	176
116-	3	122.5	3.013	163
126-	18	131.5	4.240	186
136-	42	141.2	5.137	183
146-	49	149.8	6.033	178
156-	29	159.7	7.296	178
166-	9	169.7	8.504	173
186-	2	186.0	11.390	177

For the adults the value of  $n$  was 2.8. At any given length the adult was heavier than the larva. Thus, as in the case of linear growth, there are three phases in the weight-length relation. The departure from the cube law is most pronounced during the periods when linear growth rate is high, i.e. up to 75 mm. and over 120 mm.

So that comparisons might be made from one length to another, weight-length coefficients were calculated from  $k = W/L^3 \times 10,000$  at successive length intervals of 10 mm. (Tables 10 and 11). The

values obtained were then plotted against length in Fig. 6. The maximum value for  $k$  is found in the smallest larvae from 20 to 40 mm. From 71 to 80 mm. the coefficient decreases rapidly, after which the rate of decline slackens until a minimum value of 122 is reached at a length of 120 mm. The trend is then reversed and the value rises to 154 at 170–180 mm.

The adult coefficients are much higher at all lengths, but show a tendency to decrease with increasing length over the part of the curve where numbers are adequate. While only four metamorphosing specimens were weighed, the values obtained were intermediate between adults and ammocoetes.

significant change in length during transformation. That the increased value of the weight-length coefficient is associated with sexual maturity rather than metamorphosis would appear to be borne out by the work of Young & Bellerby (19), who found that injection of anterior lobe pituitary in ammocoetes of *L. planeri* led to the development of characters associated with sexual maturity and in particular a change in body form from a slim to a swollen condition, an effect which was more marked in specimens already metamorphosed.

The higher value of  $k$  in the few metamorphosing specimens when compared with the largest ammo-

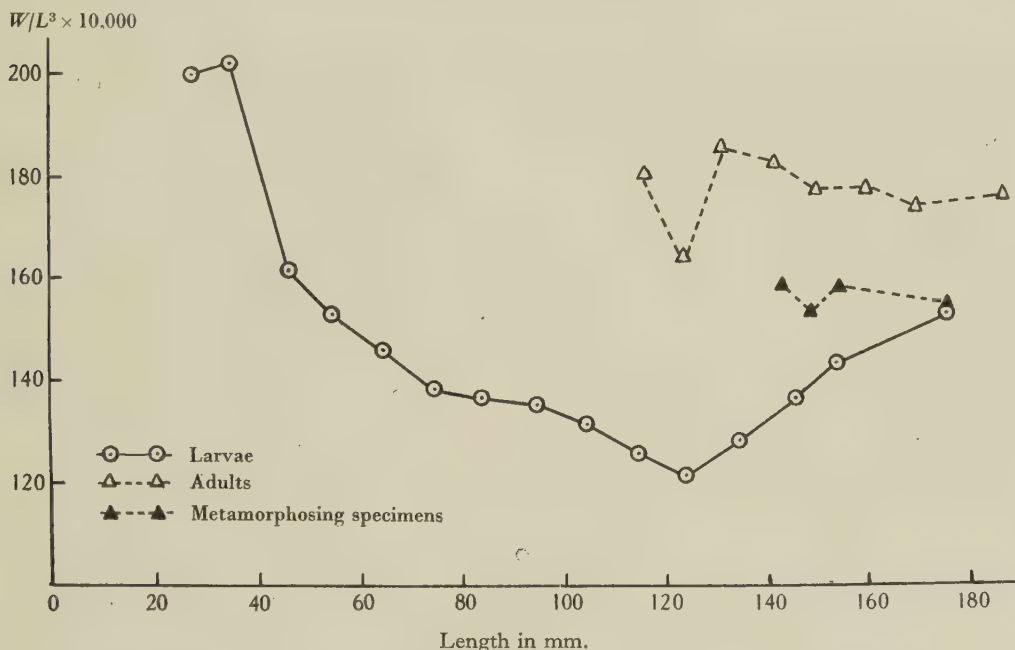


Fig. 6. Changes in the weight-length coefficient  $W/L^3 \times 10,000$  with increasing total length.

As regards growth in length and weight three phases may therefore be distinguished:

(1) The initial period of about  $1\frac{1}{2}$  years when linear growth is most rapid, proceeding at a greater rate relative to increase in weight.

(2) From  $1\frac{1}{2}$  to about  $2\frac{1}{2}$  years linear growth falls off and the rate of decline in the weight-length coefficient is reduced.

(3) A final period of acceleration in both linear growth and increase in weight, with the latter relatively the greater as shown by the rising values of  $k$ .

The greater value of  $k$  in the adults cannot be due to further increase in weight after metamorphosis and must therefore imply a reduction in length such as Cotronei (1) has established for both *Petromyzon marinus* and *Lampetra fluviatilis* at sexual maturity. Measurements of metamorphosing specimens kept under observation in tanks have failed to show any

coetes suggests that the inflexion in the weight-length curve at 120 mm. and the subsequent upward trend may be connected with the processes leading up to metamorphosis and in particular the development of the gonads.

#### 4. SUMMARY

1. Lampreys frequently spawn at exactly the same places from year to year.

2. It is suggested that the following factors are involved in the location of the spawning grounds: shade, depth of water, swiftness of the current, barriers such as weirs and waterfalls.

3. The spawning temperature has been found to lie between 10 and 11°C.

4. There is some segregation of the ammocoetes, due to the washing out of larvae from sites where the

current is swift, and the consequent accumulation of older larvae in more protected situations, where the presence of vegetable debris also provides a richer food supply. Thus a high proportion of the older larvae is often associated with a greater growth rate.

5. The evidence from the frequency curves indicates a larval period of  $3\frac{1}{2}$ –4 years and a total life span of 4 or 5 years.

6. The rate of growth in length is greatest during the first  $1\frac{1}{2}$  years, declining during the following year, but increasing again in the final stages.

7. The relation of weight to length does not follow the cube law. Increase in weight is up to 120 mm., less than the cube of the length, while beyond this point it is greater.

8. Change of form, as indicated by changes in the weight-length factor, is most marked during the phase of rapid growth.

9. The difference in the value of the weight-length coefficient for fully grown ammocoetes and adults leads to the conclusion that a reduction in length occurs at sexual maturity.

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## A STUDY OF THE ANT FAUNA OF A GARDEN, 1934-42

By B. D. WRAGGE MORLEY

(With 3 Maps in the Text)

## 1. INTRODUCTION

This paper is the result of eight years' continuous study of the ant fauna of a garden at Bournemouth. In the earlier years the author's knowledge of ants was slight, but references to species observed in these years have been carefully checked. During this period the garden has been mapped on several occasions, and the ant nests, together with the areas of domination of the various nests, plotted. I have collected these data on three maps covering the periods 1934-7, 1938-40 and 1940-2 respectively.

The garden has a southern aspect and the slope is indicated in Map 1. The soil is of a uniform sandy texture. The species of ants present in the garden have remained constant throughout the whole period, although two attempts were made to introduce new species. These will be referred to later.

Six species of ant were present in the garden:

*Acanthomyops (Donisthorpea) niger* L.

*A. (Dendrolasius) fuliginosus* Latr.

*A. (Chtonolasius) mixtus* Nyl.

*Formica fusca* L.

*Myrmica ruginodis* Nyl.

*M. scabrinodis* Nyl.

Of these the first one and the last three named are common throughout the country, while the remaining two are more local in distribution, although not uncommon. Indeed, *Acanthomyops mixtus* is, as pointed out later in the paper, probably much more widely distributed than is supposed.

## 2. SURVEYS

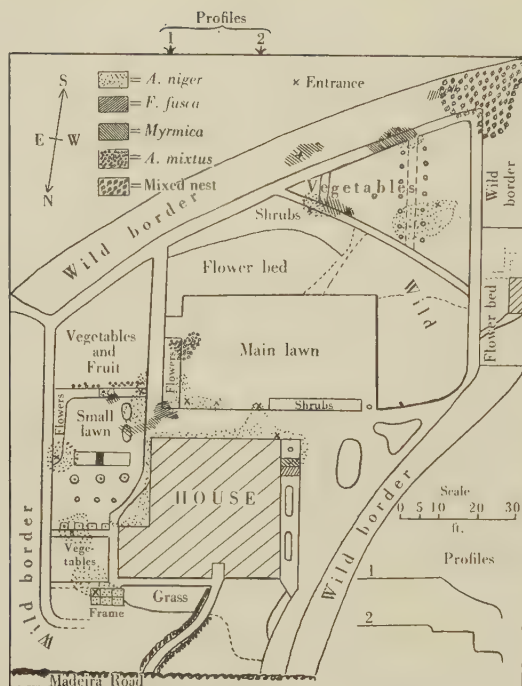
1934-7. In the south-west corner of the garden amongst the wild border of pine trees, bracken and brambles, interspersed with occasional sycamore trees, which surrounds the whole garden, was an area of territory occupied by a mixed nest of *Acanthomyops fuliginosus* and *A. mixtus*; the former a shiny jet black and the latter rather smaller (*c.* 0.6 cm. long) and yellow in colour, being closely related to the common yellow ant of the meadows—*A. flavus*. The nest itself did not appear to be in the garden, but was situated just outside it over the fence. Crawley & Donisthorpe (see Donisthorpe, 1927, pp. 222-5) have demonstrated that such mixed colonies represent the intermediate stage in the foundation of new colonies of *fuliginosus*; the *fuliginosus* queen being accepted into the nest of *A. niger*, *umbratus* or *mixtus* after the

nuptial flight and her eggs and larvae being tended by the workers of the host species. The queen of the host species is killed either by the *fuliginosus* queen or by her own offspring, and the colony becomes eventually a pure *fuliginosus* one.

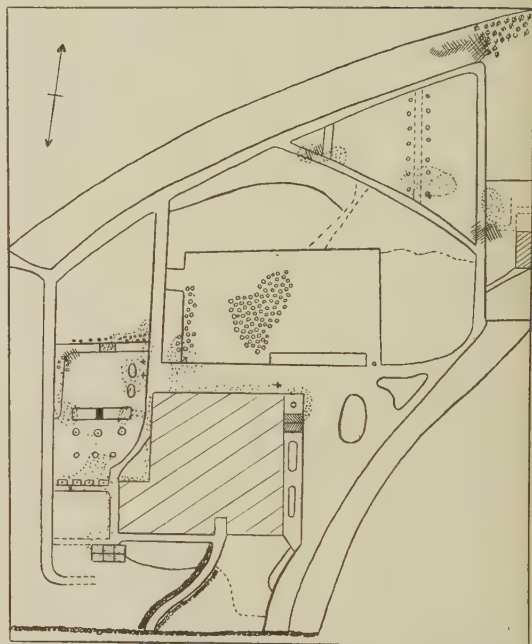
It was this nest which caused me to start my experiments on producing artificially multiple mixed colonies of several species of ants (Morley, 1940), one of which, containing nine different species, I exhibited to the Royal Entomological Society in May 1940 (*Proc. R. Ent. Soc. Lond.* (1940), Ser. C, 5: 18, 23). Further experiments have been summarized in a later paper on the nest odours of ants (Morley, 1941-2).

Ants recognize their fellow ants from the same colony, and conversely of course enemy ants, by means of their 'nest odour'. Many complex theories have been put forward concerning both the production and the appreciation of these nest odours.

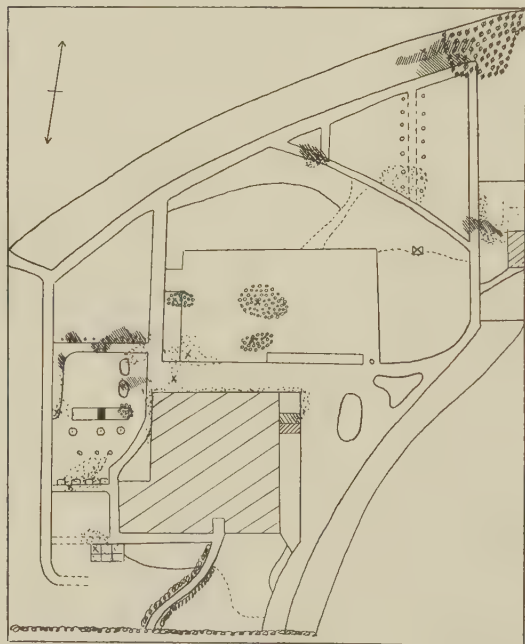
Undoubtedly ants have a very highly developed sense of smell, but I think this problem of the recognition of friend and foe has been made unduly complicated. *A. fuliginosus* is one of the relatively few species of ants which have a noticeable nest odour, and it was observed in studying the colony that the *mixtus* workers seemed to have got covered with the *fuliginosus* odour, even to the extent of seeming to be impregnated with it (Morley, 1939). This and the finding of solitary workers of *Formica fusca* and *Myrmica scabrinodis* walking unharmed on the tracks of this mixed *fuliginosus-mixtus* colony, led me to start on the experiments I have referred to and caused me finally to reject these complex theories of nest odour for the following more simple explanation: 'that there is a basic species odour, probably produced by a glandular secretion which may be expressed on to the cuticle, or is at any rate in some way exposed to the air, and that the individuality of the nest odour is imparted by slight deviations from the true species odour brought about by the ants licking one another, by their encounters with other ants and myrmecophiles, by their food and the materials from which the nest is made and other extrinsic factors'. The relationship between the *mixtus* and the *fuliginosus* appeared to be very intimate: workers of both species ascending the trees on which the aphides were pastured, although *mixtus* was not actually observed to milk the aphides (Morley, 1938*b*). This is of interest in that *mixtus* is



Map 1. Showing garden and nests with areas of foraging for the years 1934-7.



Map 3. Showing garden and nests with areas of foraging for the years 1940-2.



Map 2. Showing garden and nests with areas of foraging for the years 1938-40.

normally an entirely subterranean species, shunning the light except at the time of the annual nuptial flight. Donisthorpe (1927, p. 226) records a similar occurrence in the case of a mixed *fuliginosus-umbratus* nest. The *mixtus* workers were not found on the tracks until several weeks after the first appearance of the *fuliginosus* workers in the spring.

A few workers of both species were transferred to a plaster observation nest in order that the relationship between the two species might be better observed. In this nest a *fuliginosus* worker was observed to regurgitate honey to a *mixtus* worker and a *mixtus* worker to clean a *fuliginosus* worker, in fact the relationship was of the closest.

During this period (1934-7) the proportion of *fuliginosus* to *mixtus* was about 40 to 1 and the number of *mixtus* was gradually decreasing.

In the same corner of the garden and also in the wild part were colonies of *Formica fusca* and *Myrmica scabrinodis*, and it was from these nests that the frequent interlopers on the tracks of the mixed colony came. The former species was the more frequent visitor to the *fuliginosus-mixtus* territory, indeed the two territories overlapped. The habits of *fusca* and *fuliginosus* are, however, markedly different; for while the former is omnivorous and the workers go out singly to hunt for food (either other insects, the excreta of aphides, or the nectar from flowers), the latter feeds almost entirely on the excreta of aphides

and coccids, which it may sometimes be seen carrying from tree to tree, or from nest to tree, and it forms tracks from the nest to the neighbouring trees and bushes on which they are to be found. These tracks are thickly peopled with ants throughout the day—empty ants going towards the trees (chiefly sycamores in this case) and ants with full crops and swollen gasters returning.

On the few occasions that *Myrmica scabrinodis* and *Formica fusca* were seen to meet they took little notice of one another and 'passed by on the other side'. Besides the nest of *scabrinodis* already mentioned there was another one near some raspberry canes (south central). Here again intermingling with the inmates of the nearby *Acanthomyops niger* nest was noticeable, the *scabrinodis* wandering freely in the territory of the *niger* except in the immediate vicinity of the nest.

A solitary nest of *Acanthomyops mixtus* occurred in the cultivated part of the garden on the east side of the main lawn.

In the south-west corner of the small lawn the territories of *Myrmica ruginodis*, *Formica fusca* and *Acanthomyops niger* overlapped. The *niger* were part of what appeared to be a large polycalic colony which spread round the south and east sides of the house to the north side of the small lawn and the frame. Known entrances are marked with crosses on the map. The excavations were partly under the gravel of the path, the lawn, the foundations of the house and in the woodwork of the frame. The *Formica fusca* nest was under a large stone (unlike the first *fusca* nest which was in a decaying tree stump), while there were several nests of *Myrmica ruginodis* under the bricks of a brick path and a small piece of crazy paving round an apple tree on the south side of the small lawn. The colonies of *ruginodis* and *scabrinodis* are usually small, more especially so in the case of the former, consisting of two to three hundred and two or three queens. It is of interest that in 1936 I observed winged sexual forms present in the nest of *niger* (below the entrances worked at the south-west corner of the house) as early as March, although the nuptial flight did not take place until several months later. Donisthorpe (1927, p. 279) records that Forel found a large number of winged females of *Acanthomyops mixtus* at Morges on 16 March 1868, which he states must have over-wintered in the nests. Both sexes were present in this case and it would seem unlikely that it was a case of over-wintering.

1938-40. The nest of *Formica fusca* which was situated at the corner of the flower bed by the small lawn disappeared. The large *Acanthomyops niger* colony spread farther over the small lawn from the north, but overground contact between the nests on the south side of the house and these northern nests ceased. The *niger* outpost on the main lawn near the north-east corner of the shrubs (rhododendron bushes) disappeared and an *Acanthomyops mixtus*

nest was situated near that vicinity. Another large *mixtus* colony occupied the centre of the main lawn.

The north-east corner of the main lawn near the gravel path and the flower bed was during most of this period bare of grass, probably owing to the activities of aphides kept underground by the ants.

It is interesting to note that the *mixtus* of the main lawn and neighbouring flower bed were entirely troglodytic in their habits, while those living in parabiosis with the *fuliginosus* were conditioned to foraging above ground with their partners. The subterranean habits of the *mixtus* made it difficult to plot the extent of their territory.

The *Myrmica ruginodis* territory on the brick path was now at the height of its influence, having spread as far as the south-east corner of the small lawn, where it nested in the earth of a flower bed. Although the *Formica fusca* disappeared from the more northern part of the garden during this period it seemed to be able to hold its own against the single *Acanthomyops niger* colony near the hut (south-west, built in 1935-6) and was still to be found intermingling with the *Myrmica scabrinodis* on the *Acanthomyops fuliginosus* tracks.

During 1939 an attempt was made to introduce *Formica rufa* L. into the wild part of the garden, but unsuccessfully—probably owing to the failure to obtain a queen.

In the next year some *Tapinoma erraticum* L.—two queens and three or four workers—from a colony kept in an observation nest were placed in the garden near the hut, but were never seen again. They were released on account of the difficulty of feeding them in captivity, the queens eating their eggs and the workers gradually dying. The only food they seemed to touch was freshly killed centipedes, but even when an adequate supply of this food was available the colony was still unthrifty.

1940-2. This last map shows several interesting features. The *Myrmica ruginodis* almost completely disappeared from the brick path during this period owing to the encroachment of the *Acanthomyops niger*. I observed that while the bricks above the nests remained firm the *ruginodis* seemed to be secure from *niger* encroachments on their territory, but if the bricks were lifted and the soil slightly loosened the whole colony was soon massacred by the *niger*.

Yet the *A. mixtus* spread right along the edge of the lawn to the *niger* nest and succeeded in establishing themselves in the brick path, turning out the *niger* from part of it. The *mixtus* also strengthened their hold on the north-east portion of the garden where the *ruginodis* had practically disappeared. The position of the *Myrmica scabrinodis* and *Acanthomyops niger* nests near the raspberry canes remained stable, while the *A. fuliginosus* territory had greatly decreased in size. At the end of this period no *mixtus* workers were present, the colony having apparently reached its final stage of pure *fuliginosus*.

I believe the record of *A. mixtus* from Bournemouth is a new one. This ant would appear to be much more widely distributed than is supposed, since the author has also taken it in a garden at Reading, Berkshire, and on the Heights of Abraham at Matlock and in Dovedale in Derbyshire, there being no previous records of this species from either of these counties.

The first ants to be seen out in the spring were the two species of *Myrmica*, which would often be seen out foraging on the warmer days throughout the winter—even during December and January. *Acanthomyops niger* and *A. fuliginosus* both appeared early, although later than the *Myrmica*; while the *Acanthomyops mixtus* of the mixed colony did not usually appear on the tracks until about a month after the *fuliginosus*. The last species to make its appearance was always *fusca* which was rarely seen until late in May.

### 3. NESTING HABITS

Various types of nest and nesting sites have already been described for some of the species. The following is a complete summary of the different nest architecture and localities for each species throughout the eight years.

(a) *Acanthomyops fuliginosus*. The true nest of this species was not in the garden and was not seen. A temporary nesting place near one of the trees visited consisted of excavations round and partly in the rotten stump of a tree (below the bark). Numbers of ants of both *fuliginosus* and *mixtus* were found here at all hours of the day, even late in the evening when the tracks were no longer peopled. Some of the ants probably slept here at night during the summer months.

(b) *Acanthomyops mixtus*. One nest of this species has already been discussed in connexion with *A. fuliginosus*. This ant was found nesting under the main lawn, under the brick path and in a flower bed at various times during the period. All the nests were entirely subterranean and excavations to a depth of 7 in. showed little more than the entrance passages. The nests under the brick path were at an equal if not greater depth, the bricks merely acting as extra covering, not as solaria to catch the sun and warmth as in the case of *Myrmica*. Except in the case of the mixed nest these ants were never seen above ground, although they might be found at the surface round the entrances to their nest, where they were hidden by the grass.

(c) *Myrmica ruginodis*. *M. ruginodis* was found nesting chiefly under thick stones (2-2½ in. thick), bricks being typical of the thickness apparently liked, as against the thin stones usually preferred by the *Acanthomyops niger*. I have observed this liking for a thicker type of stone than *A. niger* and *A. flavus* also on the hillsides near Bath (Morley, 1938a). The nest is simple, consisting of a few chambers and

passages hollowed out below the stone and a few deeper chambers excavated during the colder weather. The ants rarely descended deeper than 4 in. even in midwinter. When nesting in a flower bed the nest is equally simple, a thin layer of earth taking the place of the brick.

(d) *Myrmica scabrinodis* was found nesting in a cultivated bed under a thin layer of moss, where its nest resembled that of *ruginodis* described above. In the latter case its nest was similar to that of *ruginodis*, the moss supplying the covering given by the brick or stone.

(e) *Formica fusca*. This was found nesting twice under stones and once in the stump of a rotten tree. The nests were simple and as in the case of the *Myrmica ruginodis* often of short duration, the ants flitting to another stone nearby or disappearing altogether, although the nest in the rotten stump remained throughout the whole 8 years. This is of interest in that Pickles (1940), from observations on *Formica fusca*, *Myrmica ruginodis* and *Acanthomyops flavus* at Thornhill, Yorkshire, states that the ants seem to be 'continually moving about on the area and migrations to and from the surrounding land must occur'.

(f) *Acanthomyops niger*. The nests of this ant were a complex series of galleries and chambers below the gravel path and the foundations of the house, the lawn and in the woodwork of the frame. In the case of the nest near the raspberry canes which was situated half-way up an earthen bank, a small solarium made of earth surrounding grass, about 3 in. high by 4 in. diameter, was formed. All the nests were of a permanent character.

### 4. SUMMARY

1. The ants' nests in a 2½-acre garden at Bournemouth, and the territory of the various colonies have been carefully mapped over a period of 8 years, and summarized in three maps covering the periods 1934-7, 1938-40, 1940-2. The soil was sandy, and the garden had a southern aspect.

2. Six species of ants occurred in the garden, the number of species remaining constant throughout the period: *Acanthomyops (Dendrolasius) fuliginosus* Latr., *A. (Donisthorpea) niger* L., *A. (Chtonolasius) mixtus* Nyl., *Formica fusca* L., *Myrmica ruginodis* Nyl., *M. scabrinodis* Nyl.

3. A mixed colony of *Acanthomyops fuliginosus-A. mixtus* occurred in one corner of the garden. The *A. mixtus* died out until the colony reached its final stage of development in 1942 when it was pure *A. fuliginosus*.

4. The *Acanthomyops mixtus* in the mixed colony ascended the trees to 'milk' aphides with the *A. fuliginosus*, abandoning the usual troglodytic habits of this species, which, however, were maintained by the large *A. mixtus* colonies elsewhere in the garden.

5. Workers of *Formica fusca* and *Myrmica scabrinodis* were observed wandering unharmed on the tracks of the mixed *Acanthomyops fuliginosus*-*A. mixtus* colony. Intermingling of foraging workers of *Myrmica scabrinodis* and *Acanthomyops niger*, and *Myrmica ruginodis*, *Formica fusca* and *Acanthomyops niger* was also observed.

6. Winged forms of both sexes of *Acanthomyops niger* were observed in the nest in March 1936, although the nuptial flight did not occur until several months later. It is unlikely that these sexual forms had over-wintered.

7. The success of the various species of ants, measured in terms of the area they foraged over and dominated, fluctuated greatly throughout the period. These fluctuations are indicated and discussed. Large polycalic colonies such as those found in the case of *Acanthomyops mixtus* and *A. niger* seemed to

be more successful than the single nests of *Myrmica* and *Formica fusca*. The latter also appeared much less permanent in character. The troglodytic *Acanthomyops mixtus*, however, succeeded in turning the *A. niger* out of parts of the garden towards the end of the period.

8. The types of nests inhabited by each species are discussed.

## 5. ACKNOWLEDGEMENTS

My thanks are due to Mr Donisthorpe for the help and encouragement which he gave me during the early years of my myrmecological studies; and I must also acknowledge the help of Miss Prudence Wragge Morley and Master Peter Wragge Morley in finding the ants' nests.

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# TERRITORIES AND INTERRELATIONS OF TWO ANTS OF THE GENUS *MESSOR* IN ALGERIA

By W. PICKLES

(With 1 Figure in the Text)

## 1. INTRODUCTION

During the summer months of 1943 a survey of the territories and interrelations of four species of ant was carried out on an area of ground on the wild uncultivated part of a hillside in eastern Algeria. Adjacent to this area on the same hillside, but some distance away, two nests of ants of the genus *Messor* were kept under observation from May 1943 until December 1943 when observations were concluded.

The two species of ant were, at nest A, *M. barbarus* L. and at nest B, *M. aegyptiacus* Emery *canaliculatus* Donisthorpe, the two nests being separated by a distance of 18 ft. (see Fig. 1). These ants are very similar in their habits, both being harvesters and both making long processions out to the places where their grass seeds are being harvested.

## 2. TERRITORIES

As these species are harvesters, both permanent and temporary trackways were made. In Fig. 1 the foraging area and the tracks made by the ants from nest B are illustrated. These were not all permanent ones, but those recorded on specific days. The tracks of the ants from nest A were not mapped out, as more detailed observations on the territories of *Messor barbarus* were made on other parts of the hillside which will be published elsewhere. From the results obtained in this other survey, the foraging territory of *M. barbarus* was found to be 7857 sq.yd., with a maximum foraging distance of 150 yd. from the nest.

At nest B the maximum distance to which these ants travelled was 82 ft. from the nest. This may be taken as the radius of a circle of foraging activities of 2348 sq.yd., foraging taking place roughly equally in all directions.

On several occasions processions from nest B were formed, leading over the mound of nest A and proceeding beyond it, so that the presence of these ants at nest A did not prevent those from B from foraging in this direction. On a few occasions only, ants from nest A were observed foraging in the direction of nest B—generally they were single ants only. Here then were two related species of ant with similar habits foraging over the same ground, the whole of the foraging territory of nest B being within that of nest A.

## 3. INTERRELATIONS OF THE TWO SPECIES OF ANT

It was observed on several occasions when processions of ants were proceeding from nest B over and beyond nest A that the ants of the latter nest avoided those from the former nest; but on 22 August 1943 at 6.30 p.m. (D.B.S.T.), the first real battle between these two species was witnessed. At this time of the day the battle appeared to have been in progress for a

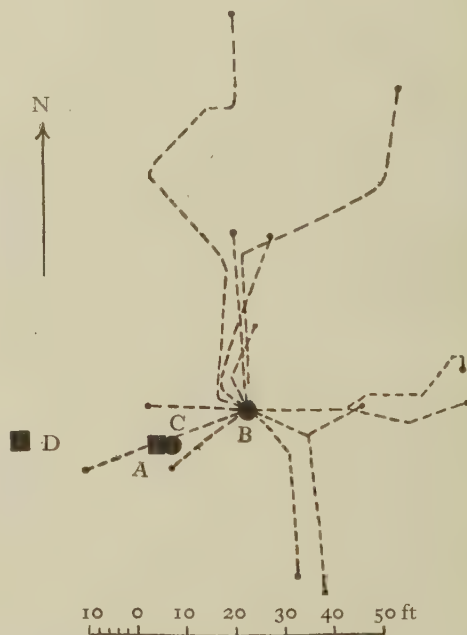


Fig. 1. Plan of the trackways leading from nest B (*Messor aegyptiacus*): large disks represent nests of this species and squares those of *Messor barbarus*.

considerable period of time, because there was an area of ground about 1 yd. square which was packed tightly with ants from nest A, all very excited and darting with jaws agape at the invaders from nest B. There were pockets of skirmishes in various parts of this writhing mass of ants. The inhabitants of nest A were so excited that they would even dart at their own fellows when they approached each other; but they did not attack each other or grapple with each other as with the invader. Soldiers were busy carrying off

bodily the invaders that they had captured. At 8.15 p.m. (D.B.S.T.) the battle was still in progress, but there were fewer ants abroad and there were only a few ants from nest B attacking. By 8.30 p.m. (D.B.S.T.) the invaders had returned to their own nest and there were very few ants abroad at nest A; these were still in an excited condition.

On 20 September at 6 p.m. (D.B.S.T.) there was another battle in progress at nest A, the invaders being again ants from nest B. There were not so many ants of either species abroad as on 22 August when the first battle was witnessed; but on this occasion *M. aegyptiacus* was excavating a hole at a spot 4 ft. due east of nest A, whilst others were attempting to invade the nest at A. Amongst the mêlée of ants there were clusters of *M. barbarus* rolling over and over in an attempt to get an invader thrown out of the precincts of the nest. This battle raged for several days, because when observations were made at this spot at about 6.30 p.m. (D.B.S.T.) on 22 and 24 September the ants were still fighting. It is difficult to say whether there had been continuous fighting during this time or not, at least during daylight; but on 24 September most of the openings of nest A were barricaded with large pieces of soil and stones.

For 10 days (20–30 September) the ants from nest B were excavating at the spot 4 ft. from nest A, this temporary nest being marked C in Fig. 1. Apparently for some reason or other the enterprise was abandoned on 30 September. At this spot the ants spent all their time excavating and there were no records made of foraging; the only ants abroad, when they came into contact with any *M. barbarus*, would commence fighting. On 26 September there were a number of soldiers of *M. barbarus* abroad without abdomens, and still quite lively. On this date the amputation of the abdomen of several soldiers and small workers of *M. barbarus* by the other species was witnessed.

From 24 September until 8 October, whenever the nests were visited, the mouths of nest A were stopped up with stones and pieces of soil; but on this date all the mouths of nest A were open. At nest B excavating was now in progress. When the area was next visited at 1.45 p.m. (B.S.T.) on 10 October there was a procession of ants from nest A to a spot 27 ft. from it and almost due west. Although the procession was still in progress from this nest to the new spot (marked D in Fig. 1), excavation was already going on at the new spot. Only very few ants were returning from D to A.

From this date onwards nest A was completely deserted, and the mouths became sealed up with soil falling in after rainstorms, and by early December the whole nest was obliterated completely by the elements.

It seems likely that the movement of *M. barbarus* from nest A to nest D was an attempt to escape from the invader, but it is strange that these ants should choose a site still within the territory of nest B. Until the end of this survey the ants at nest D were busy excavating a nest. There was no foraging from this nest, as it was established at the end of the harvesting season and the commencement of the rainy season.

At the close of this survey the state of affairs was that nest A was deserted and nest D was a flourishing colony of *M. barbarus*, whilst the temporary nest C was abandoned and obliterated and the original nest B was still an active colony of *M. aegyptiacus*.

#### 4. GENERAL OBSERVATIONS

Like *M. barbarus*, *M. aegyptiacus* had a siesta during the heat of the day and during the summer months which corresponded closely in the hour of the day and duration during the summer with the former species. In a similar manner to *M. barbarus*, a midden of the husks of grass inflorescences was made by *M. aegyptiacus*.

Swarming of *M. aegyptiacus* was observed on 6 October 1943 at 2 p.m. (B.S.T.), winged males and females issuing from the nest. This ant seems to have an enemy in the shape of the ant *Camponotus rufo-glaucus* Jerd *micans* Nyl. At the nest of this species, on 6 October at 6 p.m. (B.S.T.), workers of *Camponotus* were dragging into their nest winged females of *M. aegyptiacus* and were also biting off their wings and amputating their abdomens.

#### 5. SUMMARY

1. The foraging activities of the ant *Messor aegyptiacus canaliculatus* were observed from May till December 1943 and its trackways were mapped out. The territory was calculated to be 2348 sq.yd.

2. Their nest was 18 ft. away from a nest of *M. barbarus barbarus* and therefore the foraging territory was entirely within that of the latter (7857 sq.yd.).

3. On many occasions these *M. aegyptiacus* were observed to invade the territory of the *M. barbarus* and battles were recorded. Finally, after a temporary nest lasting 10 days had been established by the former, the latter evacuated their old nest (A) and moved to a spot 27 ft. away (outside but near the territory of *M. barbarus*) and settled down to excavate a new nest there. There they remained until the end of the survey.

#### 6. ACKNOWLEDGEMENTS

I wish to express my thanks to Mr H. St J. K. Donisthorpe for naming the ants for me; and Mr Charles Elton for assistance in connexion with arrangement of the paper, reading proofs, etc.

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# THE DOMESTIC CAT AS A FACTOR IN URBAN ECOLOGY

By COLIN MATHESON, *Department of Zoology, National Museum of Wales*

## 1. INTRODUCTION

Though it is generally believed that the introduction into this country, and into Europe generally, of the cat as a domestic animal, was of considerably later date than that of the dog, yet its introduction is certainly of great antiquity. According to Mivart, 'there can be no question as to the Cat having been domesticated in Europe before the Christian era. There are signs that it was domesticated among the people of the Bronze period' (10); but precise information is still lacking. In this country, remains which were considered, after careful examination, to belong to the domestic rather than the wild cat, and tiles on which, while still soft, cat footprints had been impressed, have been excavated from the Roman city at Silchester in Hampshire (2, 3, 6); and in central Europe, according to Sieber, who has examined prints on Roman tiles from Stillfried a.d. March (North Austria) and from Eisenstadt in Burgenland, 'Durch das Vorkommen dieser Fährten auf römischen Ziegeln wird zweifellos belegt, dass die Hauskatze spätestens im 2. bis 3. Jahrhundert n. Chr. in Mitteleuropa schon gehalten wurde und, wie es scheint, nicht allzu selten'. After the second and third centuries, he states, the next sure evidence of the presence of house cats in central Europe is found about the year 600 A.D. (11). In the Middle Ages, the great value set upon the cat 'is shown by the laws which in Wales, Switzerland, Saxony, and other European countries, imposed a heavy fine on Cat-killers'. The first known written mention of the domestic cat in this country occurs in the code of laws attributed to the tenth-century Welsh prince Hywel the Good, according to which, 'Whoever shall kill a cat which guards a barn of a King or shall take it stealthily, its head is to be held downwards on a clean level floor, and its tail is to be held upwards; and after that, wheat is to be poured about it until the tip of its tail be hidden [and that is its worth]. Another cat is four legal pence in value' (12)—the same value as assigned to a sheep.

In seventeenth-century London, with its old wooden buildings which provided numerous retreats for mice and the house-haunting black rat (*Rattus rattus*), cats were no doubt an important factor in rodent destruction; but apart from such doubtful figures as those mentioned by Defoe in his *Journal of the Plague Year* we have no indication of their numbers. W. H. Hudson's remarks also, on the cat population of London at the end of the nineteenth

century, were obviously intended only as rough suggestions (4).

## 2. SCHOOL QUESTIONNAIRE

In view of the not unimportant role of the domestic cat in urban ecology to-day, an attempt has been made by the writer to obtain as close an estimate of its numbers as possible for the city of Cardiff. For this purpose information was sought, in the spring of 1944, from a number of schools representing all areas of the city, and including both elementary and secondary schools. The masters and mistresses co-operating were asked to obtain from each pupil under their charge the following information, and to tabulate it in columns: (1) the total number of people at present resident in his or her house, and (2) the number of cats kept in the house; the first column being, of course, filled in whether or not any cats were kept. Care was taken as far as possible to prevent duplicate entries for the same household, in cases where two or more children from the same family were attending one school, and also to include only the number of cats normally kept and not newly born litters; while in general, to make the figures more dependable, infants' departments were not included. Lists were received from thirteen schools, and the information is tabulated in Table 1.

The variation in these figures is much what might be expected, having regard to the different localities and types of schools concerned. School A, with the highest proportion of cats and cat-keeping households, is in the docks area of Cardiff, in old property with a racially mixed population. Schools B, C, D and E are also in fairly old parts of the city, inhabited by a working-class population; the area served by school F includes some newer property. As regards the secondary schools, the position is rather different, the pupils there being of course not necessarily from the immediate neighbourhood, as is generally the case with the elementary schools: they come from various parts of the city, but will mostly be the children of parents who might be expected, on the whole, to live in a rather better type of house.

It will be seen that in the homes of these children the population of cats is generally somewhat lower—on an average 9.5% as against 11.0% for the elementary schools. This difference is probably attributable to several factors, which will suggest themselves fairly readily, but the relative importance of which it would be difficult to assess.

### 3. DECREASE ON MUNICIPAL HOUSING ESTATES

Perhaps the most striking figures, as illustrating the influence of municipal building developments on the keeping of domestic animals, are those for elementary schools G and H. Both these schools serve and are situated in corporation housing estates built since 1920; these consist of semi-detached houses the great bulk of which have been occupied for 15 years or longer, and there are no restrictions on the keeping of domestic pets such as are in force in some towns in many tenement houses, and in large blocks of flats

the Cardiff Chief Sanitary Inspector from 252 premises in various parts of the city during April 1944; and not one of them came from the housing estates served by these schools. This is by no means the only factor influencing the keeping of cats, but it is certainly one of them.

The same tendency for a decrease of household animals in modern housing estates is illustrated by the figures for four schools at Newport, Monmouthshire, kindly obtained for me by Dr David Oates, Director of Education for Newport (Table 2).

School N is one of the oldest schools in the town, and school O is also in the old part of Newport;

Table 1. *Proportion of cats in the homes of school children in various parts of Cardiff*

School	No. of households represented	Total no. of people in households	No. of cats kept	Cats as percentage of people	Percentage of households keeping cat or cats
Elementary School A	85	539	82	15.2	74.1
" B	239	1,277	185	14.5	62.3
" C	300	1,599	202	12.6	55.7
" D	209	1,266	158	12.5	62.7
" E	254	1,470	175	12.0	54.3
" F	112	557	61	11.1	41.1
" G	400	2,156	162	7.5	34.3
" H	144	867	48	5.5	30.6
Secondary School I	274	1,171	141	12.0	?
" J	358	1,716	172	10.0	43.0
" K	?	1,366	124	9.1	?
" L	291	1,222	105	8.6	30.9
" M	384	1,691	137	8.1	32.8
Thirteen schools	—	16,897	1,752	10.4	—

Table 2. *Proportion of cats in the homes of school children in Newport*

School	No. of households represented	Total no. of people in households	No. of cats kept	Cats as percentage of people	Percentage of households keeping cat or cats
Elementary School N	269	1,942	283	14.6	76.2
" O	210	1,210	152	12.6	58.6
" P	260	1,476	178	12.1	56.5
" Q	179	810	52	6.4	26.2

such as those built by the London County Council. Nevertheless, it will be seen that the population of cats is only from one-third to one-half as much as in the areas covered by our other elementary schools, and lower even than the figures for the secondary schools. Here, the better sewers and drains and the more modern construction of the buildings are factors which, as perhaps to some extent in the houses of secondary school children, conduce to the reduction of rodent pests and diminish the need for cats as destroyers of rats and mice. It may be mentioned that following a recent publicity campaign in connexion with the Ministry of Food's rat-destruction work, when all householders were urged through the press and the cinemas to notify the authorities of cases of rat infestation, complaints were received by

school P is in the centre of the town, while school Q serves one of the municipal housing estates.

In using the ratio of cats to people (10.4%)\*

\* There remains the question how far this ratio, from households with children, is valid for all households. The comment of one teacher that it might be somewhat high because of children's fondness for pets is offset by that of another, whose pupils in more than one instance reported no cats of their own, but mentioned 'the old lady living alone next door' with two or three; and the bias of our school sample, as above stated, is towards a minimum percentage. Cases of a large number of cats being kept in a small household come to public notice from time to time—see, for example, a prosecution for nuisance recorded in the *Annual Report* for 1938 of the Brighton Medical Officer of Health, p. 35; and another reported in the press of 24 July 1944.

reached in Table 1, as a basis for estimating the cat population of the whole city of Cardiff, it may be noticed that this ratio, being calculated from figures of which an undue proportion relate to secondary schools, is therefore probably rather low; while it is possible also that the number of cats kept at present is somewhat below the normal owing to food-supply difficulties. It is used here, however, in order to avoid any likelihood of an over-estimate; and on the basis of the normal population of Cardiff (estimated at 226,100 in 1940) means a total of at least 23,500 cats.

#### 4. STATISTICS OF STRAY CATS

In addition, account must be taken of the numerous stray and unwanted cats found in every town, of which we can obtain at least a minimum estimate from the numbers destroyed each year in large towns by the Royal Society for the Prevention of Cruelty to Animals, local Animal Welfare Leagues, and similar organizations. In Cardiff, data collected through the courtesy of such bodies indicate that the average number of cats destroyed each year in this way during the five-year period 1938-42 inclusive was approximately 6600, equivalent to 3% of the human population.

It appears, therefore, from the results of our questionnaire and the known statistics about stray and unwanted cats, that in a city like Cardiff, with a population approaching the quarter-million mark, the cat population must be at a minimum 30,000 or 13% of the human population.

The statistics of stray cats destroyed in Cardiff are borne out by similar information from other cities, though it is not always easy to get complete data. Nevertheless, figures which cover at least the great bulk of the humane cat-lethalization work are available for four other cities in Great Britain and America, and show that the numbers of cats thus disposed of annually may range from about 1 to over 3% of the human population. Figures kindly supplied by the two organizations concerned show that in Edinburgh (population about 473,000 in 1938) the average number destroyed in the period 1938-43 was 4550 annually (about 1%). In Glasgow in 1936, when the population was approximately 1,120,000, the number of cats known to be destroyed was 22,700 (2%)(8). In Boston (U.S.A.), with a population of 670,600 in the mid-year 1910, the Animal Rescue League destroyed, during the decade 1905-14, a total of 210,000 cats or 21,000 per annum (3%)(1). In Liverpool, including Bootle and Crosby, with a population averaging somewhat under 1,000,000 during the decade 1931-40, the number of cats received for humane disposal at the Cats' Shelters every year averaged 33,000 or over 3% of the human population (see Table 3, for which I am indebted to Mr F. J. Winchester, Secretary of the R.S.P.C.A., Liverpool Branch).

The problem of the numerous stray cats in London was discussed over forty years ago by Hudson(4), who thought their numbers might be from eighty thousand to one hundred thousand. He advocated their removal by the police to lethal chambers such as are in fact in operation in many cities at the present time. A factor which in New York, according to Laut(7), had by 1920 resulted in a great diminution in the number of 'gutter cats', was the growth of a popular fashion for summer furs and cheap furs; the pelts were dyed and in the spring sales of 1920 sold for 15 cents to 1 dollar 15 cents according to grade.

Table 3. *Animals received at the Liverpool cats' shelters, 1930-42*

Year	Number received	Litters (included in previous column)
1930	30,806	?
1931	30,675	?
1932	32,040	?
1933	32,681	?
1934	35,667	4,527
1935	37,352	4,082
1936	34,998	3,490
1937	34,184	3,074
1938	33,694	3,174
1939	34,383	3,316
1940	30,397	2,457
1941	25,311	1,776
1942	18,298	1,519

*Note.* The litters are included in the larger figures given in the previous column and are not in addition thereto; one complete litter counts as 1 in the figures. A certain number of dogs, totalling perhaps as many as 500 in a year, is included in the totals, but, on the other hand, a small number of cats is taken each year to the Liverpool Dogs' Home. The area covered includes Bootle and Crosby as well as the City of Liverpool.

#### 5. GENERAL COMMENTS

It is not proposed to discuss the effects of this large cat population on the other species in the urban fauna; studies have been published in America(1, 9) regarding the effect of cats on bird life, but the results obtained are not necessarily applicable to this country. Hudson wrote an interesting general descriptive account(4) of the influence of cats on the birds of London (without, however, any attempt at a quantitative estimate) in which he suggested that it was not entirely adverse, as many of the birds concerned were the young of the house sparrow. As regards the relations of the cat to human health, summaries of the facts so far known have been given by Hull(5) and by Henderson & Craig(1); but much more data will be needed before it is possible to present a balanced picture of the influence of the cat on the health of urban communities as a whole. As a matter of historic interest it may be worth

mentioning, in view of the former general practice in European cities of destroying cats and dogs when a bubonic plague epidemic occurred, that it has been found that neither species is very susceptible to the rodent disease; cats are stated to be only slightly susceptible to plague, and relatively unimportant agents in spreading it.

## 6. SUMMARY

An attempt was made, by means of a questionnaire to school children in Cardiff and Newport, and by consideration of the numbers of stray and unwanted cats dealt with annually by societies carrying out lethalization work, to obtain an approximate ratio of domestic cats to people in big cities; as a result the cats are estimated at a minimum as about 13% of

the human population (roughly 10½% house-kept cats, the remaining 2-3% strays). The data obtained from both towns indicate a distinct decline in the numbers of domestic cats kept on modern housing estates as compared with the older areas of towns.

## 7. ACKNOWLEDGEMENTS

The writer is greatly indebted to helpers who are too numerous to be named individually but without whose ready assistance it would have been impossible to carry out this survey; to the headmasters and teachers of the various schools, and to the secretaries and other members of animal welfare organizations in Cardiff and elsewhere. To all of them he wishes to offer his sincere thanks.

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## A TRANSECT CENSUS OF PIGEONS

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(With 2 Figures in the Text)

### 1. INTRODUCTION

Transect censuses have been little used in this country. Ocean transects of bird populations have been published and American work on land, though more particularly on mammals, has shown the possibilities of this method of census taking. In Great Britain Nicholson (1931) first seriously advocated counting birds from the train, and more recently Colquhoun (1941) has tested the validity of transects of woodland populations on a small scale. This paper attempts to show that not only can broad features of distribution and density be mapped from careful train counts and correlated with environmental character, but such results, if they are done with certain precautions, bear a constant relation to total populations and an ascertainable relation to densities.

As regards the latter two points, at least two counts over the same area should be made. This will show a certain measure of variation between counts, and simple statistical calculations reveal whether the degree of variation is of a purely random nature. If this is so, then we are justified in concluding: (1) that the two counts are samples of the same population, and (2) that parallel changes in the two counts during the course of the transect reflect within approximate limits real changes in density of the populations sampled. If the degree of variation between the counts is greater than that to be expected from chance, then one can conclude that the population or the environment has changed in some way between the counts and that neither can be depended upon to give true information about anything but the fact of change.

Of course greater-than-chance variation may creep in owing to imperfections in the counting technique. Thus, workers should be careful not only to equate conditions during the two counts (by making them at the same time of day and season and with the same number of observers, etc.), but also to state exhaustively what were the exact conditions.

### 2. METHODS

The counts concerned were made by W. B. Alexander, B. W. Tucker, J. S. Watson and the writer on an outward journey (1 July 1942) and a return journey (10 and 11 July) between Berkshire and Devonshire. The distance is about 132 miles each way and a long stretch of the pastoral uplands suspected of carrying

a dense population of wood pigeons (*Columba palumbus*) and stock doves (*C. oenas*) was crossed. The westward journey was made between 14.30 hr. (D.B.S.T.) and 19.30 hr., in fine weather; the eastward journey was made between 16.30 and 18.30 hr. on 10 July and 12.15 and 16.30 hr. on 11 July, in slightly stormy weather. On the westward journey two observers counted birds on one side of the train and two on the other; on the return journey both sides were examined on 10 July, but only one side (that to the south) on 11 July. Conditions of visibility were practically identical.

These conditions and methods fail to achieve the ideal in several respects (most transects will, but it is worth while having clearly in one's mind the conditions to aim at). The return journey was unavoidably broken; this in itself did not matter, but it meant that the times of day did not coincide with the outward trip, and also that there were not sufficient observers to cover both sides of the line on 11 July (only three were present).

### 3. POSSIBLE ERRORS INVOLVED

These are the bare circumstances under which the counts were made. Since the main purpose was to determine whether discrepancies between the two counts were only such as could be explained by the normal variation of random sampling (in other words whether the two samples gave consistent and therefore true pictures of the populations sampled) it is worth considering the possible factors, which could produce large (i.e. greater than random) errors in the counts. In general such errors, if envisaged beforehand, might be (a) important enough to discourage the taking of the count at all, or (b) avoidable by making adjustments in the technique of counting or analysis.

In the first place unequal distribution might have made the two counts discrepant. This might occur through change of habitat, e.g. during the westward journey hay had just been cut, and during the return journey most of it had been carried. If two species are included in the counts, errors may be involved through one preferring to feed in newly cut hay. Actually the results show that this was not so. Again, movement of flocks may produce unequal distribution, which would affect the validity of the results. Here an adjustment should probably be made in the

analysis, but the point is academic and may await the considered opinion of a competent statistician.

In the second place unequal conspicuousness may bias the counts. We cannot then compare the relative density of the two species counted, unless we know how much more conspicuous one is than the other. Colquhoun (1941) has made an interesting analysis of this matter as far as woodland birds are concerned. In the present instance, however, the two species chosen are as nearly equal in conspicuousness as two British species can be, so that the question does not arise.

Apart from this, care must obviously be taken to avoid making two counts in which the environment is not comparable because of seasonal change in cover, changed weather conditions or alteration of habits.

Mr M. K. Colquhoun, who has kindly read and criticized this paper, has suggested that in these samples care must be taken over interpretation because of the incomplete correspondence of the times at which the two journeys were made. Thus, although the fact that the return journey was started in the evening and finished in the afternoon brings it more into line with the outward journey than if it had been completed in one day, nevertheless there is a discrepancy of about 3 hr. The counts for the outward journey made in § 6 (see Appendix) ending at 19.30 hr. (D.B.S.T.) may therefore run into the evening feeding time of the two species, and this fact may account for the larger number seen on the first journey. Thus, in Fig. 2 the small rise in the curve for both species towards the end may give a slightly exaggerated idea of their density compared with the previous part of the curve.

In these samples greater accuracy must be attributed to the numerical relations between the two species than to the geographical change in total numbers, though the latter undoubtedly reflect within approximate limits real changes in density. Nevertheless, where there is an evening feeding period, this should, if possible, be excluded from observations.

It has rather been assumed in the previous paragraphs that it is best to count more than one species. This is not essential, of course, but in analysing the results it is distinctly advantageous to have two classes of data which will cross-check.

#### 4. NATURAL AREAS TRAVERSED

(a) The Kennet Valley. Reading–Hungerford, *c.* 22 miles. The first 10 miles run through the flood plain (160–190 ft.) which is pasture and reed beds. This narrows through Newbury and on to Hungerford, rising to 330 ft., while the flanking terraces close in on the valley. Almost to Hungerford these flanks carry mixed farms and forest. Towards Hungerford a grain-clover region is entered.

(b) Vale of Pewsey. Hungerford–Lavington, *c.* 24 miles. For about 10 miles the line crosses high ground, the Bedwyn grass-forest region, which reaches up to 460 ft. Poor pasture, forest and scrub heath. Then the Vale of Pewsey proper is on Upper Greensand (200–350 ft.) and supports mixed farming. There is a good deal of grass with arable interspersed. Crops are mostly beans, roots and green fodder.

(c) Lavington–Bruton, *c.* 24 miles. For most of this stretch the line runs across the Oxford Clay Belt, varying between 200 and 350 ft. It follows the lower ground most of the way and has steep hillsides closing in. This is predominantly pasture with a good deal of woodland.

(d) Bruton–Somerton, 12 miles. The line runs down (240–40 ft.) gradually through the Lower Scarplands (Oolite) and the Lias Clay pasture regions into the levels, where the flood plains of the Carey and the Brue push fingers across. Here arable increases.

(e) Somerton–Wiveliscombe, *c.* 25 miles. The largest part of this area is low ground comprising first the levels round the river Parrett and then the valley of the Tone beyond Taunton to Norton Fitzwarren (20–100 ft.). Most of the lower ground is pasture, but there is more arable wherever it rises slightly. The slopes close in west of Taunton, where the Keuper marl slopes with their high proportion (for this part) of arable flank the river and the railway.

(f) Wiveliscombe–Filleigh, *c.* 28 miles. Practically all this area is on dry well-drained Red Sandstone, whose permanent pasture is the main feature of the landscape. The highest ground is only a few miles from Wiveliscombe (539 ft.), and after Dulverton the line slopes down into the valley of the Yeo. Here there is more rough pasture, especially to the south of the railway, but most of the ground is still meadowland. There is little extensive woodland, but the country generally with its valleys and coombes is well wooded.

#### 5. GENERAL RESULTS

In Fig. 1 the number of wood pigeons per cent. total is given. The general picture is so striking that it needs no analysis to make plain the broad lines. Stock doves are very common throughout the whole of the area, and only in the last section are they less than 60% of the total. In the middle part of the transect they rise to and maintain a quite astonishing preponderance.

Generally speaking the peak of the stock doves seems to coincide with the high open chalklands with their rough pasture and patches of woodland. The wood pigeon seems to prefer the country at the beginning and end of the journey, where the landscape is more generally wooded. It is, however, very difficult to find any more definite correlation between the

see-saw of the two species and particular environmental factors.

Then the remarkably high density of pigeons throughout the transect should be noted. Altogether close on 400 birds of both species were recorded on the two journeys; the average rate therefore is about 1.5 birds per mile including built-up areas and

possible to draw anything but general inferences from these figures, because among other things birds were probably more conspicuous at this season owing to their liking for hay fields. That the population on these uplands is a dense one, however, seems clear.

In Fig. 2 the distribution of the density is analysed in more detail. The journey is here divided into equal distances without regard for the natural areas, and the figures for every 20 miles are given. The total number of birds seen only falls below 40 in one 20-mile section, while on the Wiltshire uplands it

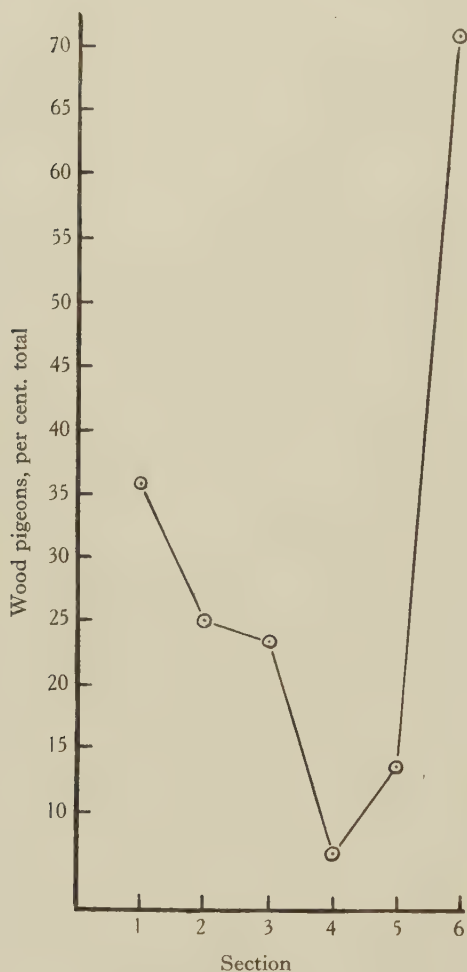


Fig. 1. Percentage of wood pigeons in each section (both journeys). (Sect. 1: 36.6; sect. 2: 25.0; sect. 3: 23.5; sect. 4: 6.9; sect. 5: 13.6; sect. 6: 71.6).

cuttings, where the view was obscured. I have had occasion to travel through other parts of England keeping a look-out for pigeons, but have never come across a density comparable with this. On outward and return journeys between Oxford and Liverpool in April the total number of pigeons seen was not above 30, and from Oxford to Reading (just before the counts, which are the subject of this paper, started) only two birds were recorded. It is not

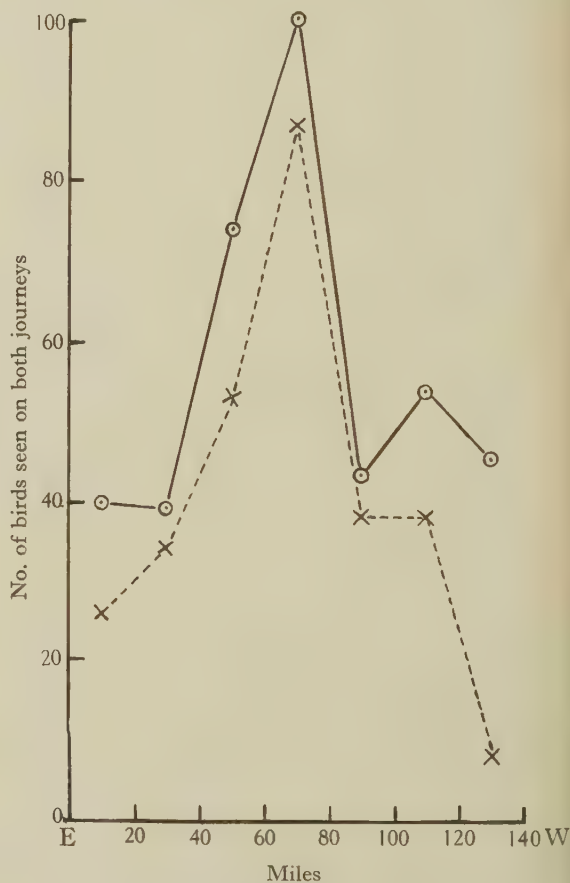


Fig. 2. Totals of both species (unbroken line) and of stock doves (broken line) per 20 miles.

rises to 100, or 5 birds per mile. The second curve shows the total number of stock doves observed in each 20 miles. This again demonstrates the great preponderance of this species in this part of the journey. As mentioned above, it is not possible to relate this sample to the total population, which remains unknown, but it is possible to show that distribution of density reflects a real change in total numbers in the different sections of the transect, with the possible exception of the last (see p. 135).

## 6. STATISTICAL TESTS

In Table 1 are given section by section the numbers of each species seen on each journey. By applying the  $\chi^2$  test with Yates's contraction for continuity (Fisher, 1934) one can determine whether the difference between the figures for each journey is statistically significant, i.e. whether it is due to causes other than chance. If the difference is not significant, then the counts reflect accurately the relative frequencies of the two species throughout the journeys. Taking  $P$  (probability) = 0.05 as the upper level of significance (this means that the observed difference could occur by chance once in 20 samples), five out

a description of the limits of the range. The density contours within that range are only vaguely known; all this detail badly needs filling in before we can begin to approach any more fundamental study of wild population problems.

## 7. SUMMARY

1. Counts of wood pigeons (*Columba palumbus*) and stock doves (*C. oenas*) taken from a train during two journeys between Berkshire and Devonshire show that the former species is more abundant at the western end of the stretch of country observed,

Table 1. *Analysis by natural areas of the relative proportions of both species on both journeys*

		Wood pigeon	Stock dove	Total
Section 1. Kennet Valley $\chi_e^2 = 0.15$ ; $n = 1$ ; $P = 0.95-0.9$	Journey W	12 (10.97)	18	30
	" E	3	8	11
		<b>15</b>	<b>26</b>	<b>41</b>
Section 2. Vale of Pewsey $\chi_e^2 = 1.75$ ; $n = 1$ ; $P = 0.5-0.3$	Journey W	12 (15)	48	60
	" E	10	18	28
		<b>22</b>	<b>66</b>	<b>88</b>
Section 3. Lavington-Bruton $\chi_e^2 = 8.08$ ; $n = 1$ ; $P < 0.01$	Journey W	15 (9.65)	26	41
	" E	1	26	27
		<b>16</b>	<b>52</b>	<b>68</b>
Section 4. Bruton-Somerton $\chi_e^2 = 1.59$ ; $n = 1$ ; $P = 0.3-0.2$	Journey W	1 (2.85)	40	41
	" E	4	27	31
		<b>5</b>	<b>67</b>	<b>72</b>
Section 5. Somerton-Wiveliscombe $\chi_e^2 = 1.54$ ; $n = 1$ ; $P = 0.3-0.2$	Journey W	2 (4.22)	29	31
	" E	7	28	35
		<b>9</b>	<b>57</b>	<b>66</b>
Section 6. Wiveliscombe-Filleigh $\chi_e^2 = 0.01$ ; $n = 1$ ; $P = 0.9$	Journey W	29 (28.7)	11	40
	" E	14	6	20
		<b>43</b>	<b>17</b>	<b>60</b>
Total $\chi_e^2 = 0.43$ ; $n = 1$ ; $P = 0.5$	Journey W	71 (67.67)	172	243
	" E	39	113	152
		<b>110</b>	<b>285</b>	<b>395</b>

of six of the sections show variation ascribable to chance. Area 3 only is discrepant, so that some factor changed the proportions of the two species between the counts. Totals for the whole journey show no variations that are not attributable to random causes.

One may conclude that, with the exception of § 3, the counts give a true picture of the relative frequencies of the two species under the stated circumstances. When one considers the number of factors which might influence the number of birds seen on two such journeys, it is a source of satisfaction that the statistical tests reveal only one small discrepancy. It certainly seems desirable, in view of this, that the method should be tested more widely for gaining knowledge of distribution of our more conspicuous species on broad lines.

In conclusion one may note that our knowledge of distribution is confined in most of the text-books to

while in the rest the latter is predominant, remarkably so in the middle part. Up to five birds per mile were observed on these Wiltshire uplands.

2. Statistical tests of the variation between the counts during the two journeys show that only in one out of six sections is this variation of a magnitude greater than would be expected from random causes.

3. It is suggested that with proper precautions and tests double transects will give a good measure of changing density throughout the region traversed, and should enable us to get a more detailed picture of the distribution of our more conspicuous species.

## 8. ACKNOWLEDGEMENTS

The writer is most grateful to Mr P. H. Leslie for help and advice with the statistical treatment of the data, and to Mr M. K. Colquhoun for criticism.

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## APPENDIX

*Actual counts taken on the two journeys*

Each individual entry or unit of observation relates to a bird or birds seen and counted together. Usually these coincided with birds in a single field, but where groups or individuals were clearly separated, even in the same field, they have been entered separately. The data are grouped according to the natural areas traversed, but since in Fig. 2 the figures are given for each 20 miles, sections of this length are also indicated by arrows.

	Journey west						Journey east								
	Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total			
Sect. 1. The Kennet Valley	3	0	3	12	18	30	1	0	1	3	8	11			
	0	1	1				1	0	1						
	7	0	7				1	0	1						
	1	0	1				0	3	3						
	0	17	17				0	2	2						
→	1	0	1				0	2	2						
							0	1	1						
							←								
Sect. 2. Vale of Pewsey	2	0	2	12	48	60	0	1	1	10	18	28			
	0	6	6				1	0	1						
	0	10	10				0	1	1						
	0	2	2				1	0	1						
	0	1	1				←								
	0	2	2				1	0	1						
	0	1	1				7	16	23						
	0	2	2												
	0	3	3												
	0	4	4												
	0	1	1												
→	6	1	7												
	0	2	2												
	0	1	1												
	4	12	16												
Sect. 3. Lavington- Bruton	0	4	4	15	26	41	1	0	1	1	26	27			
	0	3	3				0	2	2						
	0	5	5				0	1	1						
	2	0	2				←								
	0	2	2				0	6	6						
	0	4	4				0	6	6						
→	0	2	2				0	2	2						
	0	2	2				0	2	2						
	13	0	13				0	1	1						
	0	1	1				0	6	6						
	0	3	3												
Sect. 4. Bruton- Somerton	0	2	2	1	40	41	0	3	3	4	27	31			
	0	2	2				0	4	4						
	0	6	6				0	7	7						
	0	2	2				0	4	4						
	0	10	10				←								
	0	14	14				0	6	6						
→	0	2	2				4	3	7						
	0	2	2												
	1	0	1												

			Journey west						Journey east					
			Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total	Wood pigeon	Stock dove	Total
Sect. 5. Somerton- Wiveliscombe	o	6	6						o	2	2			
	o	2	2						o	1	1			
	o	2	2						o	4	4			
	→								o	10	10			
	o	3	3									←		
	o	6	6						o	2	2			
	o	2	2			2	29	31	1	0	1		7	28
	1	0	1						1	0	1			35
	o	1	1						1	0	1			
	1	0	1						1	0	1			
	o	4	4						3	0	3			
	o	2	2						o	3	3			
	o	1	1						o	6	6			
Sect. 6. Wiveliscombe- Filleigh	o	3	3						o	1	1			
	o	1	1						o	2	2			
	1	0	1						2	0	2			
	2	0	2						o	1	1			
	→								1	0	1			
	15	1	16						1	0	1			
	1	0	1									←		
	o	1	1			29	11	40	6	0	6		14	6
	1	0	1						o	2	2			20
	3	0	3						1	0	1			
	3	0	3						2	0	2			
	1	0	1						1	0	1			
	1	0	1											
	1	0	1											
	o	5	5											

# SLUGS IN GARDENS: THEIR NUMBERS, ACTIVITIES AND DISTRIBUTION. PART I

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(With 18 Figures in the Text)

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### 1. FOREWORD

The purpose of this paper is to give the results of studying natural populations of slugs in certain gardens at Harpenden, a village on the chalklands at the edge of the Chilterns, lying half-way between St Albans and Luton and about 25 miles north of London.

The need for this investigation arose as the result of experimenting with various substances which might be of use with metaldehyde in the control of slugs (Barnes & Weil, 1942). The interpretation of these experiments was seriously hampered by the lack of definite information of the specific make-up and the activities, especially seasonal, of slug populations.

The present authors have found that the collection of slugs when they are active is the best method of gaining such information. Consequently, this has been the main source of the data. Incidentally, it should be emphasized that it is the number of slugs which are active, not necessarily the absolute population, that determines the extent of damage done. It is hoped that the results of this study will further the growing trend of opinion that such ecological studies are the logical and highly desirable first approach to pest control.

Correct specific identification is of paramount importance. For this reason, § 2 is devoted to certain points concerning the species and their recognition, with a key for the separation of the common species.

Part 1 continues with descriptions of the areas investigated and the method employed, as well as an explanation of the manner in which the data are presented. The abundance and seasonal activity of the various species occupy the rest of this Part, which is concluded by a short summary. The findings in this Part are well established and do not call for any further research in the immediate future, at all events in the Harpenden area.

Part 2 (to be published in this *Journal*, vol 14, no. 1, 1945) contains many extremely interesting

facts, obtained in the course of this investigation, which call for further research. For instance, at the beginning there is a description of the feeding habits as observed while collecting the slugs. This indicates the need for an inquiry into their food requirements. Next there is a section on the mating time and breeding season as seen after nightfall. Although the mating time is shown to be linked up with the seasonal activity, there is obviously much that cannot be obtained by direct observation after dark. The succeeding section demonstrates how closely the weights of slugs are bound up with their seasonal activity, mating time and breeding season. But here again definite investigations on the rates of growth are indicated. The distributions of the species within the district are next shown to be remarkable, and the elucidation of the underlying causes would clarify many problems concerned with the occurrence of slugs. The evidence put forward regarding the times of nocturnal activity in relation to the season of the year, as well as of the different species, demands further investigation. Finally, the information gained concerning the effect of local weather conditions on the general activity of slugs indicates the need for more exact observational studies and points to an experimental approach. This Part is also concluded by a summary.

The Appendices contain the full data concerning the after-dark collections of the slugs.

Considerable numbers (99,601) of slugs have been dealt with in the course of these investigations. This fact is indicated in Table 1, which shows the development of the study.

Acknowledgements for particular help are incorporated in the text, but it is a pleasure to take this opportunity of placing on record the benefit obtained by personal meetings and interchange of views and results with two other workers on slugs: Mrs Barbara H. Dainton, who has been investigating the underlying causes of activity in slugs, in the Zoological Department, Cambridge; and Mr D. C. Thomas,

who has been working in the South-Western Advisory Province on methods of sampling slugs and their control under field conditions. The latter's wide knowledge of slugs in general has been most helpful.

## 2. THE SPECIES INVOLVED

The following nine species have been found in Harpenden in the course of the present investigation:

Arionidae	<i>Arion ater</i> (L.)
	<i>A. circumscriptus</i> Johnst.
	<i>A. hortensis</i> Fér.
	<i>A. subfuscus</i> (Drap.)
Milacidae	<i>Milax gracilis</i> (Leydig)
	<i>M. sowerbyi</i> (Fér.)
Limacidae	<i>Agriolimax reticulatus</i> (Müll.)
	<i>Limax maximus</i> L.
	<i>L. flavus</i> L.

that what we at first took to be *A. intermedius* was not this species at all. It was later proved by Mr Thomas by means of dissection and by Mrs Dainton and the first-named author by breeding experiments, that these bright-coloured small slugs were none other than the young of *A. ater*. As the result of this error, we have been able to keep separate the records of young *ater* from the older specimens of this species.

A further point regarding the identification is worthy of note. It involves the *Milax* species, *gracilis*, *gagates* and *sowerbyi*. Here again we are indebted to Mr Thomas, who most kindly pointed out that the slug we were identifying as *gagates* was *gracilis* and also sent us living specimens of the three *Milax* species from Devon. Apparently many of the older records of *gagates* must be considered as referring to *gracilis*, which was only recognized as

Table 1. *Development of the study*

Year	Baiting		Night and twilight collections			Other methods	
	Experiments	Slugs	Samples	Nights	Slugs	Experiments	Slugs
1940: April–August	15	8,659	—	—	—	—	—
1941: June–September*	5	4,703	2	1	200	—	—
September–December	2	659	11	8	1,391	—	—
1942	23	7,299†	203	126	35,838‡	7	449
1943	4	1,503§	181	119	38,416	3	484
1940–3	49	22,823	397	254	75,845	10	933

\* Up to 10 September 1941 the slugs dealt with were not separated into species, but since that date, which begins the period covering this paper, specific determinations have been made on every occasion.

† This includes 1805 slugs which were observed and identified but not removed from the garden involved (see footnote \* to Table 4).

‡ Of these 832 were collected at twilight.

§ This includes 190 slugs which were observed and identified but not removed from the garden involved (see footnote † to Table 4).

Other species mentioned are *Arion intermedius* (Normand) (pp. 141, 145), *Milax gagates* (Drap.) (pp. 141, 143, 145), *Agriolimax agrestis* (L.) (pp. 144–5), *Agriolimax* sp. (? *carvanae* Poll.) (p. 145), *A. laevis* (Müll.) (pp. 144–5), *Limax cinereoniger* Wolf (pp. 144–5), *L. marginatus* Müll. (pp. 144–5), *L. tenellus* Müll. (pp. 144–5), and *Geomalacus maculosus* Allman (p. 145).

The first-named author, while taking responsibility for the identification of the slugs, is most grateful to Mrs Barbara H. Dainton and Mr D. C. Thomas for their invaluable help. Both paid the authors visits and discussed the salient points. The former identified most of the 1941 collections and checked several later samples that had been separated into the different species at Harpenden. By this means it was found that at first there was a liability to confuse the small specimens of *Arion circumscriptus*, *A. hortensis* and *A. subfuscus*. Later these errors were reduced to negligible proportions.

To Mr Thomas we are indebted for pointing out

occurring in the British Isles as recently as 1930 (Phillips & Watson, 1930). We have not yet found the true *gagates* in Harpenden. In addition to this confusion of *gracilis* and *gagates*, we have discovered that in one collection *sowerbyi* has been labelled as *gagates* and *gracilis* as *sowerbyi*. Finally, Dr H. W. Miles, when discussing slugs with us, unhesitatingly used the name *sowerbyi* for specimens of *gracilis* and *gagates* for specimens of *sowerbyi*. This suggested that, when *sowerbyi* was stated to be most abundant in the Manchester district, the species in reality was *gracilis* (Miles, Wood & Thomas, 1931). *M. gracilis* and *gagates* were left out of these authors' list of economic species. This possibility is enhanced by the fact that when R. Aileen Barr (1926) investigated the pedal gland of *Milax*, she referred to the species which had been collected in Manchester as *sowerbyi*, but it was later pointed out by Phillips & Watson (1930) that the species with which she dealt was in fact *gracilis*.

It is proposed to deal now with each of the nine

species found in Harpenden gardens, pointing out the characters used by us in recognizing them and also giving notes on their variations, size and appearance of young as observed during this study.

#### *Arion ater*

This is the common Black Slug of the hedgerow and roadside. The more mature specimens have been recognized by their size, the coarseness of the tubercles, the usual uniformity in coloration and the habit of humping up into a hemispherical attitude when disturbed. A further characteristic used is the curious elephantine swaying motion during which it lurches from side to side when irritated by repeated touching.

In the course of this study no record has been kept of the frequency of the colour varieties encountered, but black, grey, almost black with orange fringe, white with orange fringe and chestnut red specimens of the adults have been found, while orange, straw-coloured, greenish yellow, grey and chestnut as well as black smaller individuals have been seen. Mature specimens have been met measuring a good 6 in. in length as they move along, though it is recorded elsewhere that they attain 8 in. (20 cm.).

Newly hatched individuals are almost orange in colour and remain a straw tint until about 1 in. in length, but the tentacles are dark.

The straw-coloured individuals have predominated in the early part of the year, i.e. January to March. During the spring, i.e. from April onwards, the larger specimens have been encountered more and more frequently, until in the summer (June and July) scarcely any young have been found. In August the young straw-coloured individuals start reappearing. Throughout the winter months these young specimens have formed the bulk of the *A. ater* populations. In late September and October some of the mature slugs have exhibited a quite definite old 'moth-eaten' appearance which has been taken to foretell their demise in the near future. Mr Thomas, however, has suggested that these marks may have been caused by individuals nibbling each other during courtship and mating.

#### *Arion circumscriptus*

This is Bourguignat's Slug, recognized by its usually grey coloration, with a dark band on each side, depressed or flattened appearance and very white foot. The only species with which it has been liable to be confused is *A. hortensis*, from which it has been distinguished by the facts that its foot is never yellowish, its general colour is lighter, its black markings are obvious, its body is flattened dorso-ventrally and inclined to be relatively broader, and its skin is not so tough or slimy. In size it is about the same as *A. hortensis*. The only variation encountered has been a general brownish or reddish colour.

#### *Arion hortensis*

The common Garden Slug. The Harpenden specimens were distinguished by a black or rusty black colour and the foot being always yellow or orange of some shade. It has been separated from *A. circumscriptus* by its tougher skin, the darker coloration, the orange foot, the absence of well-defined lateral bands, and the lack of a depressed appearance; from young *A. ater* by its dark colour and smoother integument; and from young *A. subfuscus* by the difference in coloration and the presence of a definitely yellow or orange foot. The most noticeable variations have been the different intensities of the general black appearance and the colour of the foot, which has varied from deep orange to an extremely pale yellow.

In size, the largest specimens have been usually about  $\frac{3}{4}$  in. in length, but have reached almost twice this when moving. Under dry conditions, such as occur frequently during the summer months, individuals appear attenuated, whilst under moist conditions they are definitely more plump.

Newly or very recently hatched individuals have been found throughout the year. Similarly, medium and full-sized specimens have been collected during every month of the year. In other words, any sample of this species collected at any time of the year under favourable conditions almost certainly will contain specimens of all sizes. This is an important fact when trying to assess the damage caused by slugs using the weight of 100 individuals (see Part 2, § 10). For information on the twilight activity of the young of this species reference should be made to Part 2, § 12.

#### *Arion subfuscus*

This is the so-called Dusky Slug. It has been recognized by the fact that its colour is always some shade of brown dorsally. It has been distinguished from *A. ater* by its generally smaller size; its body is inclined to be flattened, more smooth and longer proportionally in shape, particularly when at rest; its banding is obvious usually; and its foot is nearly white. Only the smaller specimens are likely to be confused with *Arion circumscriptus* and *A. hortensis*, and it has been distinguished from the young of the former species by its brown coloration and the fact that its foot, although very pale, is not dead white. Likewise it has been separated from young *hortensis* by its brown colour dorsally, lighter on the sides, and the absence of an orange or yellow foot. The young of *ater* are separable by their rougher integument and their uniform coloration. While these distinguishing characters may appear difficult to grasp from the printed word, in practice they are quite obvious when once pointed out.

The variations in shades of brown have been noticeable. While some specimens have been dusky, others have been rufous, others bright brown of various shades and intensities, while still others have been yellowish brown and so on. In some specimens

the markings have been sharply defined, in others they have blended into the general colour.

*A. subfuscus* is a medium-sized slug. Specimens reaching 4 in. in length when moving have been collected, but more often individuals have been about 3 in. long.

Newly hatched specimens have been found in large numbers during the winter months, notably in December, January and February. In contrast, almost all the individuals found in June, July and August have been large. By September, however, small specimens have again begun to make their appearance, and from October onwards until the summer have nearly always been present. The large specimens have become progressively more infrequent in the samples from September until in the winter months they have only been found occasionally. Just as in the case of *ater*, the large specimens have exhibited during the autumn months an old, 'moth-eaten' appearance. Nevertheless, more large *subfuscus* have been found during the winter than large specimens of *ater*. Whereas this sign of having mated or of an early demise became apparent in *ater* in late September and October in 1942, in *subfuscus* it was obvious a month earlier (i.e. late August) and lasted throughout October. It would appear that most of the larger specimens of *subfuscus* which have been found during the winter months are individuals which hatched early enough in the autumn to enable them to attain considerable growth before the onset of winter. Few individuals apparently survive a second winter.

It is possible that wintry conditions may act differentially on slugs of different sizes and be more lethal to individuals above a certain size. It would follow from this that generally speaking mature specimens of the larger species would usually not survive a second winter, whereas those of the smaller ones would. As a consequence, providing there were spells of mild weather during the winter months, the smaller slugs could go on breeding over a far greater range of months than the larger species. Information on the months when mating has been observed will be found in Part 2, § 9.

#### *Milax gracilis*

This is one of the so-called 'Keeled Slugs'. It is usually attenuated in appearance when active and reaches 3 in. in length, although more often it is about 2 in. long. When hidden away during the daytime it lies folded back on itself, rather than simply constricted in length as most other slugs. It has also a pronounced tendency to congregate at such times with others of its own species. In colour it is dark, grey-black or very dark brown, lighter on the sides and with the keel only slightly lighter than the surrounding coloration. The body at the sides has a veined appearance. The foot is dark and distinctly tripartitely coloured, the central portion being

dark and the outer portions paler grey. This species is noticeably sticky and tacky, not slimy, and locally has the name 'sticky back'.

It has been separated from *M. gagates* by shape and the colour of the foot, which in *gagates* is pale and not noticeably tripartitely coloured. The general appearance of *gagates*, in living specimens as sent us by Mr Thomas, is translucent or teneral (i.e. the colour gives the impression of being about to darken as in a newly emerged insect imago); the keel is as dark as or darker than the body.

*M. gracilis* has been distinguished from *M. sowerbyi* by its dark tripartitely coloured foot, its elongate shape and the lack of lateral compression so typical of *sowerbyi*. Mr Thomas informs us that *gagates* exhibits this lateral compression sometimes to a marked extent.

The only variation found has been an almost white form of which on one occasion three specimens were attracted to a bait at No. 14 The Pleasance and of which one other specimen was collected in the garden of No. 24 Douglas Road.

Small specimens have been found in samples collected in April, but newly or recently hatched individuals have been encountered regularly from the end of July, all through the autumn and winter months. This is one of the three species (*Arion hortensis* and *Agriolimax reticulatus* being the other two) of which individuals of almost all stages of growth appear in any sample collected after dark at any season of the year. Further details are given in Part 2, § 10, where the weight of slugs is considered in relation to the amount of food they are likely to eat and the damage they cause.

#### *Milax sowerbyi*

This is another of the 'Keeled Slugs'. It is a medium-sized species, heavily built and compressed laterally. Specimens have been found reaching 4 in. in length when moving, but usually mature specimens are about 3 in. long. At rest it is squat and tall. In colour this species is minutely mottled with orange or yellow and black, giving a somewhat brown general coloration. In the winter months the general appearance of the larger specimens is darker and almost black. The actual pattern is brick-like on the sides toward the foot. The keel is lighter in colour and is sometimes distinctly orange. It is well defined, even presenting a crinkled crest-like appearance when the animal is constricted. The foot is pale, usually yellowish, and not distinctly tripartitely coloured. This slug is dry to the touch, and not so sticky as *gracilis*.

It has been separated from *gracilis* by general shape, colour and its pale foot. The first two of these characters have also served to distinguish it from *gagates*. Viewed from the side, *sowerbyi* is much taller than *gracilis*, but this is not a good character by which to distinguish it from *gagates* which, according

to Mr Thomas, also is distinctly laterally compressed. The general colour of the specimens of *sowerbyi* collected has varied from yellowish to brown to almost black.

Newly or very recently hatched individuals have been found once in June, but more frequently at the end of July, during August (most noticeably), September and October. Parallel with this it has been observed that the largest specimens were most abundant during August and September. Most of the individuals collected during the winter and spring months have been of intermediate size. But more larger-sized specimens have been encountered in this period of the year than in the case of either *Arion ater* or *A. subfuscus*. From our observations it is logical to conclude that a certain proportion survive a second winter.

#### *Agriolimax reticulatus*

This is the common Field or Grey Field Slug. In the English literature it usually appears as *A. agrestis*, but we understand that the authorities consider that authenticated records of the latter species indicate that it is not as widespread in the British Isles as was formerly thought.

It is pale whitish to brownish, mottled or speckled, and to the touch is extremely soft. In addition, when handled it exudes a milky white slime. Mature specimens have been about  $1\frac{1}{2}$ –2 in. in length when moving. It is probably the best known of the English species.

Newly or very recently hatched individuals have been collected every month (except February 1942 when no sampling could be done), but they have occurred much the most frequently during August and September in 1942 and during May, June and July in 1943.

*A. agrestis* is differentiated from *A. reticulatus* chiefly on internal characters and needs great experience to be separated on external characters only (Luther, 1915).

*A. laevis* (Müll.), the Marsh Slug, is a smaller and extremely active slug of similar general appearance, but may be distinguished by the median appearance of the mantle when fully extended owing to the unusual length of the neck. In addition, its slime is clear and watery.

#### *Limax maximus*

This species is known as the Great Slug and is only surpassed in size in this country by *L. cinereoniger*, the Ash-black Slug. The latter species is stated to measure 4–c.  $15\frac{1}{2}$  in. in length, whereas *L. maximus* is recorded as being from 4 to sometimes 8 in. in length. One specimen captured during the course of this study measured 10 in. when moving, although usually the larger specimens were about 6 in. long.

In colour the specimens found have been ashen

grey, and frequently the typical banding was more or less broken up into spots. This species may be distinguished from its congeners by the fact that *cinereoniger* has no spots or bands on the mantle, whereas in *maximus* there are only spots on the mantle, and in *L. marginatus* (= *arborum*), the Tree Slug, there are bands with or without spots. These three species are stated to produce clear uncoloured slime. The two other species, *L. flavus* and *L. tenellus*, produce yellow and thicker slime.

Too few specimens have been found to get much idea of the breeding season of *maximus*, but small specimens about  $\frac{1}{2}$  in. long have been found from time to time between October and the beginning of April, while the largest specimens have been found during the summer.

#### *Limax flavus*

Only ten immature specimens of this species, the Yellow Slug, have been encountered.

#### Key for the separation of the common species

The following key should suffice for the requisite separation of the more common species likely to be encountered. No claim is put forward that perfect identifications should be made as the result of using it. But Miss Geraldine Cope, laboratory assistant in the Entomology Department at Rothamsted, and Dr C. B. Williams, head of the department, very kindly agreed to test its use. Accordingly, both were provided with about one hundred slugs collected the previous night and asked to identify them. Each of these volunteers, who had never previously tried to identify slugs, was successful in identifying 94% of the slugs correctly. Needless to say, for more exact determinations and probably for slugs from some other areas, reference should be made elsewhere, e.g. to Taylor's Monograph (1907) or to living authorities. It appears to us that it is comparatively easy to pick up the specific differences when once they are pointed out, but it is more difficult to grasp them from the literature. The colours given in this key are the most usual, but great variation occurs, especially in *Arion ater*, which may be white or chestnut red in addition to various shades of black and grey. As will be seen, the first step to take in sorting slugs into their species is to divide them into one of three groups according to whether they have no keel, a slight keel on the posterior half of the body or a well-defined keel running centrally from just behind the mantle to the tail.\* It is easier to separate the slugs into their species when they are alive, unless one wants to resort to dissection, which is the most reliable method of identification.

\* The authors are, of course, aware that in the Arionidae the breathing hole is near the front of the mantle whereas in the Milacidae and Limacidae it opens behind the middle of the mantle-margin.

- A. No keel (or ridge) present along the middle of the back.
- B. General colour black-grey.
- C. Large (up to 8 in.\*), glossy, rough, foot (or part of the body in contact with the ground) a light shade. **Arion ater**
- CC. Small (up to 1-1½ in.), foot bright orange or some shade of yellow. **Arion hortensis**
- CCC. Small (up to 1 in.), flattened from above to below, foot strikingly white. **Arion circumscriptus**
- BB. General colour brown, with distinct markings, foot pale (up to 4 in.). **Arion subfuscus**
- BBB. General colour straw or yellow, with no distinct markings (up to 1 in.), with dark feelers. young **Arion ater**
- AA. A slight keel on posterior half of the back.
- B. General colour light grey-brown, mottled.
- C. Producing chalky white slime (up to about 1½-2 in.). **Agriolimax reticulatus** or **Agriolimax agrestis**†
- CC. Producing clear watery slime (about 1 in.). **Agriolimax laevis**†
- BB. General colour dark grey-black, producing clear uncoloured slime.
- C. No spots on the mantle (the front end of the body) (up to 15½ in.). **Limax cinereoniger**‡
- CC. Only spots on the mantle (up to 10 in.). **Limax maximus**
- CCC. Bands with or without spots on the mantle (up to 3 in. or more). **Limax marginatus**
- BBB. General colour yellowish, producing yellow slime.
- C. Mantle mottled, feelers bluish (up to 4 in.). **Limax flavus**
- CC. Mantle not obviously mottled, feelers black or blackish (up to 1½ in.). **Limax tenellus**
- AAA. A well-defined keel running centrally from just behind the mantle to the tail.
- B. Dark tripartitely coloured foot, usually long and attenuated (up to 3 in.). **Milax gracilis**
- BB. Foot pale.
- C. Keel very prominent, crest-like, paler than rest of body, body when at rest noticeably flattened from side to side (up to 4 in.). **Milax sowerbyi**
- CC. Keel as dark or darker than rest of body which is teneral or translucent in appearance, body also flattened from side to side (up to 2½ in.). **Milax gagates**

\* All the lengths given are, of course, approximate and indicate mature specimens when moving.

† See pp. 144 and 175.

‡ The keel runs farther forward in this species than in other *Limax* species, thus indicating that *cinereoniger* has a closer affinity to the *Milax* group than the remaining *Limax* species.

The above key does not include the so-called Hedgehog Slug (*Arion intermedius* (Normand)) which is a small slug, pale, banded, similar to *hortensis* but covered with spikes, hence its popular name, the Spotted Slug, *Geomalacus maculosus* Allman, which is confined to the S.W. of Ireland. Neither does it include the three species of the genus *Testacella* which possess a small shell externally on the surface of the body at the tail end. The species of this genus prey on worms, other slugs, snails, centipedes, etc.

### 3. THE AREAS INVESTIGATED

The areas sampled have been almost entirely garden ones. It is realized that by dealing with such areas certain limitations and difficulties connected with this type of investigation are accentuated. For example, the lack of uniformity in extraneous cover for slugs, soil and vegetation tends to increase the difficulties of satisfactory replication compared with sampling in fields under a uniform crop. Again, the number of slugs per unit of area is rather meaningless when applied to the number in gardens, on account

of the large percentage of paths, stones in rockeries and so on in such places. But the advantages have outweighed these drawbacks to a large extent. Thus, the time and trouble of having to go only as far as neighbouring gardens during the night is much less than would be necessary if the same number of fields had been visited. Also few farm fields under one crop would have as great a variety and abundance of slug species as an ordinary garden. This would be expected from the large number of ecological sites in a garden compared with in a one-crop field. More important is the fact that normally the whole of any garden is not in the same state of cultivation at any one time, whereas a field is. Since cultivation is one of the best methods of disturbing slugs, the seasonal abundance of these animals could not usually be studied uninterruptedly in a field for more than a few months at a time. In other words, there are practically always some parts of a garden which have not recently been drastically cultivated. Even in gardens occasionally, particularly in wartime when the man spends his infrequent periods of leave tidying up the garden, the seasonal trend of the slugs is liable to receive nasty jolts.

When discussing sampling the term 'garden' is used throughout this paper to denote that the sampling covered the whole garden or rather the slugs were collected from a fixed route, which was chosen as bringing in representative examples of the different ecological sites (see Part 1, § 4). When the term 'other places', 'places other than gardens' or 'other places than gardens' is used, it is meant to convey that allotments, a field, a glasshouse and particular parts in gardens were sampled. Thus in five gardens vegetable patches only were examined; also the potato patch in the back garden of No. 5 Moreton End Lane was sampled. Such samples are included under 'other places than gardens' and not under 'gardens'. A glance at Tables 5 and 7 will make this arbitrary distinction clear.

Most of the sampling and experimentation has been done in the Moreton End district of Harpenden (Fig. 1). Out of the 21 gardens sampled in 1942, 18 were in this district, and out of 47 gardens sampled in 1943, 45 were in it.

The gardens are of different ages. Those in Douglas Road and those on the east side of the Luton Road are the oldest, the houses having been built about 1900. The rest of the area bounded by Moreton End Lane, Luton Road and the Hemel Hempstead railway used to be dairy farmland of long standing, with the farmstead at Moreton House (now Moreton End School). The actual dairy accommodation was what is now Vane Lodge. The cow sheds, etc., were situated on what is now part of the back garden of No. 5 Moreton End Lane, while the orchard was on the rest of this property. The farm was gradually given up. With the exception of two older houses which are now Nos. 23 and 25 Moreton End Lane, building started with some houses towards the top of the lane opposite Moreton Avenue about 1925. In 1932 the dairy accommodation and the farmstead were converted into three residences, viz. Vane Lodge, Moreton Lodge and Moreton End School. The ground round the deserted farm buildings and the orchard became derelict and served as a dump for the garden rubbish from the neighbouring houses. In 1934 the farm sheds were razed and Nos. 5, 7 and 9 Moreton End Lane were built and occupied early in 1935. The rest of the houses in Moreton End Lane (No. 11-21) and Moreton Place were built about 1937. The properties in Moreton End Lane are separated from each other by full wooden fences, those in Moreton Place by wooden palings. The gardens therefore fall into different age groups, ranging from about 5 to 40 years' existence as gardens.

The Luton Road is on the site of an old river bed, and so the gardens along it lie on a flat valley bottom and their soil is gravelly. As one proceeds up Moreton End Lane away from the depression the soil becomes more and more clay-with-flints which is typical of the Harpenden district.

One garden, the back garden of No. 5 Moreton

End Lane, in this district has served as the main scene of operations, having been actually sampled roughly 50-60 times both in 1942 and in 1943.

In the former year five other gardens in the same lane and one in Douglas Road (as well as one outside this district, i.e. in Townsend Lane) were sampled ten or more times and other gardens less frequently. This was done in order to find out if the behaviour of slugs in a particular garden is fundamentally different from that in others. It will be seen in the course of this study that for all purposes, except the study of the prevalence of species in an area, it is quite safe to deal with one garden alone.

In 1943, while the main bulk of the sampling was again done in the back garden of No. 5 Moreton End Lane,\* monthly sampling was also done in pairs of gardens on the same night, i.e. this garden and that of No. 10 Douglas Road, the back gardens of Nos. 9 and 15 Moreton End Lane and also Nos. 7 and 11 in the same lane. In the same year many more gardens (39) than in 1942 (11 gardens) were visited less frequently. The purpose of the latter was to obtain more evidence on the local distribution of the various slug species.

'Other places' were sampled in 1942 only. They included five vegetable patches in various gardens including two in the Moreton End Lane district, one (No. 14 The Pleasance) on the northern outskirts of Harpenden, and one at Redbourn, which is a village lying to the south-west of Harpenden. The 'potato patch' in the back garden of No. 5 started the year 1942 as an uncultivated area on which there was a garden rubbish heap; then it was dug up and left unplanted for a short period; next potatoes and artichokes were planted on it; and later, in August and September, it was turned into a hen run, and the hens, at first two and then six, ate down the potato plants. There were three allotments in various states of cultivation and non-cultivation behind the Rothamsted Laboratories. The Harpenden Potato Club field was visited once in April when it was fallow after being old grassland ploughed the previous late autumn and before the potatoes were planted. A grass strip was left round the ploughed area and the slugs were found on this, none being discovered on the fallow area. Lastly, one cool commercial glasshouse was visited on a single occasion.

We wish to thank all the owners and occupiers of these properties for their great kindness in allowing us free access at all times of the day and night.

#### 4. THE METHOD USED

The method used has been the collection and removal of active slugs seen, without any searching or disturbing of the foliage, etc., during a tour of the area to be sampled lasting 30 min. It might be thought

\* This garden will in future be referred to in the text simply as No. 5.

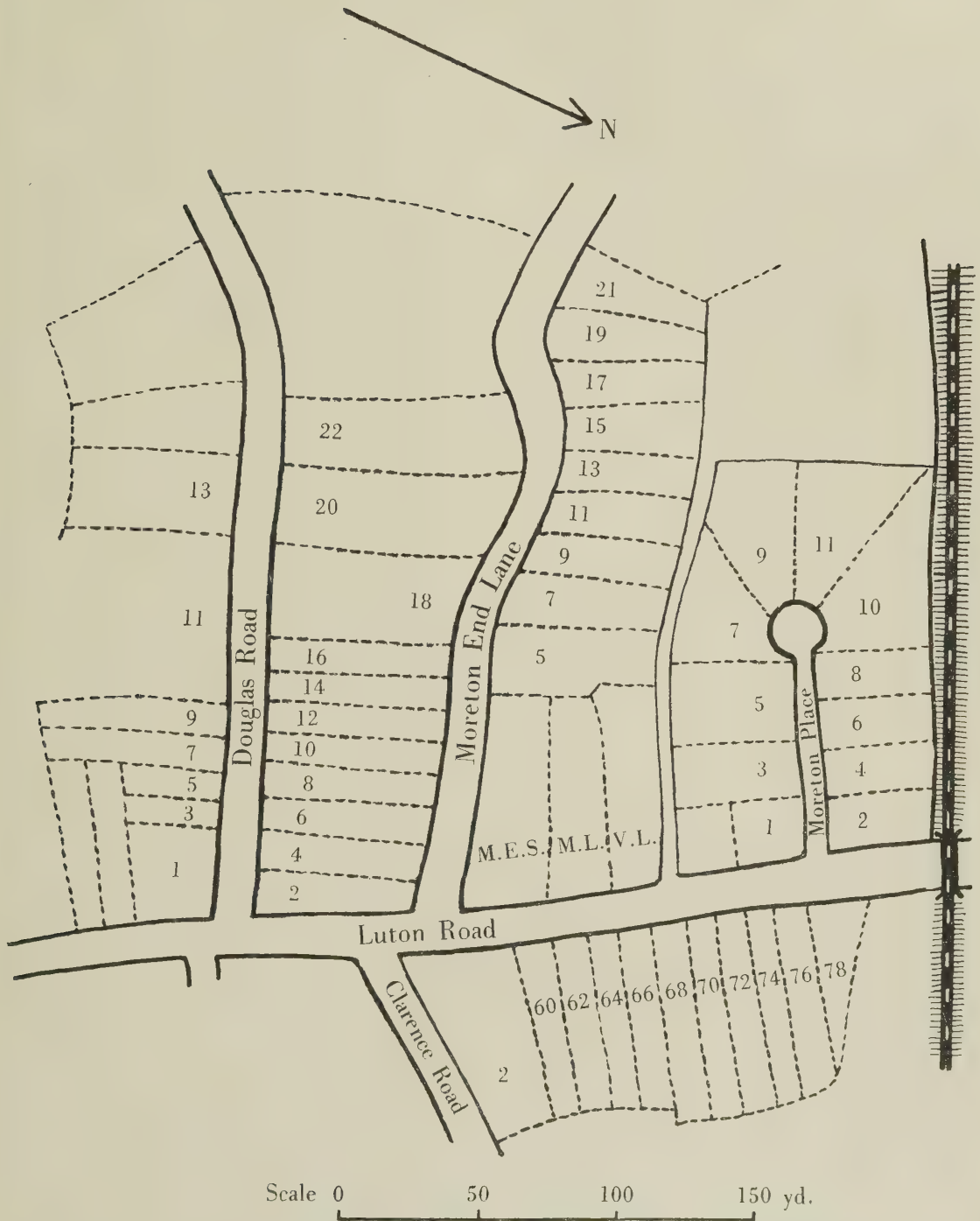


Fig. 1. Sketch-map of the Moreton End district of Harpenden. *M.E.S.* indicates Moreton End School, *M.L.* Moreton Lodge and *V.L.* Vane Lodge; otherwise the gardens are indicated by the number of the house to which they belong. The position of the numbers and letters indicates the position of the houses.

that such a simple procedure could not possibly yield reproducible results. But Table 2 shows clearly that this simple collecting method, limited by time, is perfectly capable of giving good results, i.e. the total numbers in pairs of collections are very similar and the percentages of the different species are almost identical. If certain precautions are taken, repeatable results are possible and reasonable comparisons can be made between various gardens or other areas throughout the year. Table 2 gives the results obtained by collecting twice on the same night and on successive nights in single gardens. On very few other occasions on successive nights with similar weather conditions prevailing and in no case on the same night have such collections been made: e.g. on 9 and 10 December 1941, when the collections lasted

Therefore it is not advisable, owing to the lack of uniformity in such details from garden to garden, to adopt the method of coring in gardens. Likewise any searching method would depend too greatly on the knowledge of the person concerned.

It was therefore decided to attempt to sample the slugs when they were active and moving. It was realized that owing to the nocturnal habit of slugs most of the sampling would have to be done after dark with the aid of a strong electric torch. An attempt was made to sample with a child's wooden hoop put down at randomly selected spots throughout a garden after dark. But this method, besides being exceedingly laborious, showed that it was not even always possible to place the hoop flat down everywhere. In addition, this experiment served to em-

Table 2. Collections made, using the 30 min. period after dark collecting method, on successive nights and on the same night in single gardens

Date	Time of collection (G.M.T.)	Arion				Milax		Agriolimax reticulatus	Limax maximus	Total
		ater	circumscriptus	hortensis	subfuscus	gracilis	sowerbyi			
1941										
10 Nov.	30 min.	0	0	40	9	26	3	53	0	131
11	30 min.	1	0	34	25	32	4	37	0	133
1942										
14 Mar.	21.15-21.45	3	0	99	20	35	4	20	1	182
15	19.30-20.00	2	2	106	19	28	6	24	0	187
28 Sept.	22.00-22.30	1	0	135	18	82	14	78	1	329
29	21.10-21.40	0	1	141	19	97	9	67	0	334
30 Mar.	20.30-21.00	0	0	66	5	193	5	44	0	313
30	21.30-22.00	0	0	41	4	142	0	18	0	205
25 Nov.	19.05-19.35	1	0	131	9	80	5	34	0	260
25	22.00-22.30	0	1	135	9	89	5	25	0	264
1943										
10 Oct.	21.00-21.30	0	2	137	9	371	17	34	0	570
10	22.00-22.30	1	1	142	7	337	5	24	0	517

60 min. each and on 22 and 23 December 1941, when one collection lasted 30 min. and the other 45 min. The results are comparable with those given in Table 2 and the full details are given in Appendix 1. On a few other occasions collections were made on successive nights when the weather conditions were dissimilar, with the object of demonstrating the effect of collecting under obviously unsuitable weather conditions, e.g. collecting during heavy rain (see Table 32) and during strong wind (see Table 33).

The reasons for adopting this method of sampling are as follows. If one were contemplating sampling the slugs when they were stationary or resting, as in the daytime, the method of coring or a modification of it could be adopted in open fields where most of the slugs would be down in the soil during the daytime. But in gardens, although some slugs are actually in the soil during the daytime, many others are hiding under stones in rockeries, under loose brickwork, under the edge of concrete paths, fences, etc.

phasize what had been obvious from the beginning—the complete lack of uniformity in gardens as regards hiding places (e.g. rockeries), barriers to free movement (e.g. concrete paths under certain weather conditions) and size of plants and trees.

Such diversity results in the distribution of the slugs being extremely variable during the night when they are feeding (and also during the day when they are under cover). For example, very few slugs are to be found on patches of bare soil, although they are frequently abundant immediately alongside where the food supply is more plentiful. This was amply proved in the earlier baiting experiments in which the numbers of slugs caught varied greatly from site to site, although each site was chosen previously as being a likely slug area.

With such a varied distribution, a large number of unit areas would have to be examined in order to obtain a reasonably accurate estimate of the average number of slugs per square yard or per acre. Even if this were obtained, the number of slugs per area of

garden would not mean much nor be comparable with the figures obtained for other gardens unless the exact nature of the lay-out of the garden was specified in each case.

It was therefore decided to introduce a fixed period of time during which to collect the active slugs and only restrict the area in so far as the time permitted. But obviously no two collections would be comparable if the unit of time selected were spent with no consideration of the various ecological habitats. Therefore a route in each garden was chosen to include the major different ecological habitats to be found in all gardens. Thus every garden could be assumed to have flower beds, vegetable beds, paths (either cinder, gravel or concrete), lawns, rockeries and a rubbish heap. Such places were therefore always included in the route, which remained constant for each garden every time it was sampled.

The procedure adopted was to start at the one corner of the garden, walk along the side, across the end, up the other side and finish along the house end of each garden. After a little practice the arrival at the end of the route coincided with the end of the half-hour. Naturally the length of the route traversed varied from garden to garden, as some gardens are larger than others, but the time was always 30 min. On nights when few slugs were active the torch was kept on all the time and all the area along the route in a particular garden was examined, the collector (in every case H.F.B.) moving comparatively slowly along the route. On other nights in the same garden when slugs were numerous, only patches within the area of each ecological site were illuminated, otherwise the route would not have been covered in the half-hour. The area examined thus varied according to the degree of activity of the slugs, a greater area being examined when the active slugs were few and a smaller area when the active slugs were numerous. For an absolute population study this would vitiate the method, but since this study was primarily designed to measure the activity of slugs it did not matter so long as there was some standard adopted (the 30 min. period) to ensure comparisons could be made of activity from night to night within a garden and also from garden to garden. In fact, it may be pointed out, this variation of the area accentuates the differences in the right direction for an activity study, the differences between a larger and smaller number of slugs in a collection being greater than the apparent one in that the larger collections are derived from a smaller area than the smaller ones. The paucity of slugs may be due to two causes, either to a low population or to weather conditions causing low activity at the time of the collection. Whether therefore comparisons are made between gardens in which the populations may differ, or between different occasions in the same garden when the weather conditions differ, the changes in the active

population will be greater than those actually indicated by the figures of the collections.

It may also be pointed out that the number of active slugs controls the damage actually done during any particular period, but the basic population is a measure of the potential damage. In order to measure the basic populations different methods of sampling would have to be devised. Attempts are being made in this direction, but do not fall within the scope of the present study.

The method of collecting and removing the active slugs seen without any searching or disturbing of the foliage during a 30 min. tour of the ecological sites in the area to be examined has its drawbacks. For instance, it is arduous and involves a lot of night work, especially late at night during periods of Double Summer Time. Preferably the same person

Table 3. *Sampling with (A) acetylene lamp, (B) electric torch (Exp. 54, 5 Feb. 1943). The suffix in each case refers to the 1st or 2nd half of the normal route*

Species	Number of slugs picked up					
	In 15 min.				Total	
	A <sub>1</sub>	A <sub>2</sub>	B <sub>1</sub>	B <sub>2</sub>	A	B
<i>Arion ater</i>	3	1	0	1	4	1
<i>A. circumscriptus</i>	0	1	0	0	1	0
<i>A. hortensis</i>	45	42	57	71	87	128
<i>A. subfuscus</i>	20	21	31	14	41	45
<i>Milax gracilis</i>	9	11	16	20	20	36
<i>M. sowerbyi</i>	2	1	0	2	3	2
<i>Agriolimax reticulatus</i>	13	12	14	14	25	28
Total	92	89	118	122	181	240

(as in this study) should do the collecting, and this individual should always be in the same state of health, as muscular tiredness, both of limb and eye, are likely to affect the number picked up.

Likewise the illumination used should be the same. One test comparing the use of an acetylene lamp and the electric torch has been made. The result is shown in Table 3. It will be seen that fewer of the darkest coloured species (*Arion hortensis* and *Milax gracilis*) were collected with the aid of the acetylene lamp than when the electric torch was used.

In view of the appreciable difference in the collections made with electric torch and acetylene lamp, it is probable that, even with an electric torch, some variation between collections may be caused by the running down of the battery, though this has been eliminated by replacing the batteries as frequently as possible under the wartime conditions of limited supply.

There are three important factors which affect the number of slugs picked up in a given time. They are:

(1) The time spent by the collector moving from one spot to another on his collecting route,

(2) The time spent examining the ground in the light of the torch.

(3) The time spent actually picking up and boxing the slugs.

Assuming that the time spent actually picking up slugs is directly proportional to the number picked up, then it follows that the less abundant the slugs are, the more time will be spent on (1) and (2). In other words, the smaller the collection is, the more ground that will have been covered and the more closely will it have been examined, as has already been stated.

However, the time spent actually picking up and boxing is not necessarily uniform for all species and sizes of slugs. For example, when it is not actually wet, the firmer and drier *Arion hortensis* can be collected much more quickly than the more slippery *Agriolimax reticulatus*. Similarly, very small specimens are more difficult to pick up than full-grown ones. Therefore variations are likely to occur when the relative numbers of species and the size of individual slugs vary considerably between different collections.

There are also variations in the time spent in picking up when slugs are removed from different positions, e.g. grass lawns, leaves, soil, gravel paths, etc. This variation has been eliminated as far as possible by including all these different sites on the route chosen for collecting.

These half-hour collections have been made chiefly when conditions have appeared suitable for slug activity, but also at other times such as during cold spells, dry periods, during heavy rain and so on. By this means curves have been obtained of the seasonal activity of slugs, and also data on the effect of inclement weather conditions.

Naturally the numbers of slugs collected by this method vary from garden to garden (as well as from month to month). Actually the lowest number picked up on a favourable night for slug activity after using this method in about fifty gardens in Harpenden is about 50, while the greatest number is 570. But apart from the local incidence of slugs there must be a maximum number which one can pick up in 30 min.

When slugs are extremely abundant everywhere, the time spent examining the ground and looking for them is practically nil, so that the whole of the half-hour collecting period is occupied in actually picking up and boxing slugs, apart from the time spent in moving round the route; this time also is probably reduced to a minimum. When slugs are very abundant, the numbers that can be picked up in 30 min. approaches the limit, so that differences are not observable by this method of collection when numbers are very high. Fortunately, however, in practically all gardens and for most seasons of the year, the limiting number is not approached.

Further, the possibility of subconscious selection of certain species of slugs as regards dark and light

coloration must be borne in mind. Incidentally, it may be stated that *Agriolimax reticulatus* on the soil among stones has a definite harmonizing coloration with the background.

As regards size, it is possible that the extremely small and young slugs have been missed to some extent, although on occasion large numbers of freshly hatched *Arion hortensis* and *A. subfuscus* have been collected.

The fact that large numbers of very young slugs have been picked up indicates that large variations in numbers of young may suddenly occur, and these variations may be the more marked since on subsequent collections the numbers of young may be small. It is possible that sometimes a batch of eggs may have hatched so recently that the concentration of the young is visible on the ground at the time of the collection, whereas in most other cases the less recently hatched young would have scattered over a wider area by the time a collection was made and would therefore be less likely to be observed and picked up in considerable numbers.

As regards growth of vegetation, it was at first thought that as the vegetation grew and the bare soil diminished in extent fewer slugs would be collected. But this has been proved untrue, since the greatest numbers have been picked up in the late summer and autumn, even when the fallen leaves were covering most of the ground.

Concerning species reputed to feed chiefly underground, e.g. *Milax gracilis* and *M. sowerbyi*, large numbers have been collected from time to time, but admittedly no satisfactory method has yet been devised of comparing these numbers with those feeding underground. It would be surprising, however, if any number approaching those obtained above ground were additionally feeding underground at the same time. At certain times and seasons of the year, however, large numbers do feed underground, as shown by the extent of damage suffered by potatoes.

It might be thought that continued sampling and removal of slugs might seriously diminish the slug population in an ordinary garden. Fig. 2 gives the results of sampling, by the half-hour method after dark, in the back garden of No. 5 from September 1941 to December 1943. In addition to the slugs thus removed from here, numerous other slugs have been taken out of this garden by other methods in 1940, 1941, 1942 and 1943.

In order to give the full picture of the extent to which slugs have been removed from the various localities, other known removals of slugs, 1940-3, are listed in Table 4. Previous to 1940 meta-bran baits were used occasionally in the back garden of No. 5.

Fig. 2 and the graphs (Figs. 3, 6, 9, 12 and 15) of the seasonal activity of the various species, show clearly that in no case so far has the extent of the

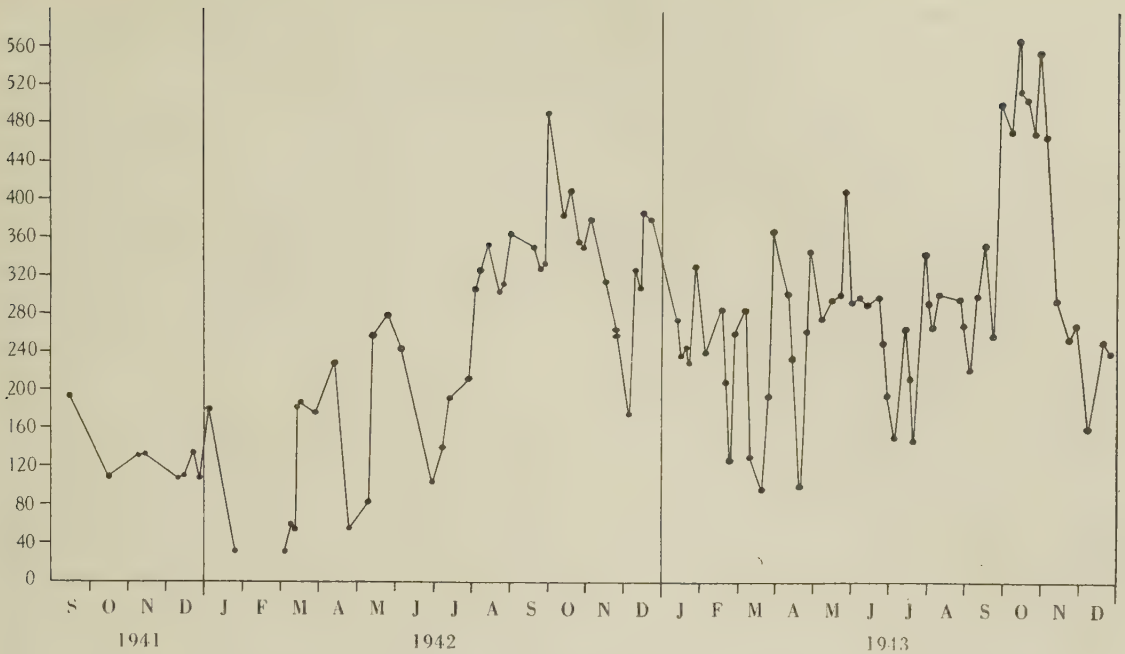


Fig. 2. Total slugs collected in the back garden of No. 5 Moreton End Lane, 1941-3.

Table 4. *Known removals of slugs, 1940-3, other than by half-hour collecting*

Year	Site	Date or period	Method	No. of slugs
1940	5 Moreton End Lane, back and front (chiefly back)	29 Apr.-7 Aug.	Baiting (Exps. 1-15)	8659
1941	Ditto	6 June-10 Sept.	Baiting (Exps. 16-20)	4703
	Ditto (back)	May	Collecting at night	c. 200
	Ditto (back)	10-11 Dec.	Baiting (Exp. 21)	473
	Ditto (front)	23-24 Dec.	Baiting (Exp. 22)	186
1942*	5 Moreton End Lane	16 Mar.-15 Aug.	Baiting (Exps. 23, 26, 33, 34, 38, 41, 43, 45, 46, 49, 50, 52)	2847
	Ditto	17-18 Mar.	Sack trapping (Exp. 25)	24
	Ditto (potato patch)	9 June and 30 July	Coring and searching (Exps. 47, 51)	52
	Ditto (front)	20 Mar.-4 June	Baiting (Exps. 29, 38, 42, 43, 45)	942
	Ditto	19-20 Mar.	Sack trapping (Exp. 27)	27
	15 Moreton End Lane	16-17 Mar.	Baiting (Exp. 24)	41
	14 The Pleasance	30 Mar.-24 May	Baiting (Exps. 31, 37, 40)	1059
	Ditto	15 and 22 May	Coring and searching (Exps. 36, 39)	145
	Ditto	30 May-17 June	Barriers (Exp. 44)	201
	Crouch Hall, Redbourn	19 Mar.-15 May	Baiting (Exps. 28, 30, 35)	591
	Glasshouse	2-3 Apr.	Baiting (Exp. 32)	14
1943†	5 Moreton End Lane (back)	21 Jan.	Replicated semicircles (Exp. 53)	170
	Ditto	2-5 Feb.	Collecting by acetylene light (Exps. 54, 60)	314
	Ditto	1-4 Apr.	Baiting (Exp. 55)	596
	Ditto (front)	2 Apr.-2 Sept.	Baiting (Exps. 56, 57)	717

\* Exp. 48 was observational only, and the 1498 slugs observed and identified in it were not removed (see Part 2, § 12) and therefore are not included in this table. Likewise in Exps. 45 and 52, 78 and 229 slugs, additional to those included in Table 4 above, were observed and identified but not removed. The total slugs therefore dealt with in the 1942 bait and other sampling experiments was the 5943 listed above which were removed and the 1805 just mentioned which were not removed, i.e. 7748 (see Table 1).

† Exp. 58 was observational only and the 190 slugs observed and identified in it were not removed and therefore are not included in this table. Likewise, Exp. 59 (in which 584 slugs were identified) was observational only. Actually it was carried out in 1944, 2-3 January, and is not included in Table 1.

sampling upset the results obtained in the later samples. It must be emphasized that this removal of slugs has been spread over a long period. If, on the other hand, it had been concentrated over a short period, the effect on the abundance would probably have been quite marked. Furthermore, the figures of 329, 334 and 492 slugs (see Appendix 1 for the times of collections), obtained in September 1942 on successive nights in the back garden of No. 5, indicate no reduction caused by repeated sampling within this comparatively short space of time. Even when sampling is done twice on the same night there is no appreciable reduction in most gardens. (Table 2 shows the intervals of time between the samples.) Thus, this same garden was sampled twice on each of the nights of 25 Nov. 1942 and 10 Oct. 1943. On the first of these nights 260 and 264 slugs were collected in the first and second samples respectively, while on the second the numbers were 570 and 517. But when the garden or area is small enough to be completely covered during the half-hour period, irrespective of the numbers of slugs active, there are indications that sampling twice in the same night results in a smaller number being picked up in the second sample. For example, 313 and 205 slugs were obtained on 30 March at No. 14 The Pleasance in two half-hour periods. Here the area was only about 10 x 10 yards and was traversed completely more than once in each collecting period.

Taken as a whole, collecting with an electric torch for 30 min. has proved to be a satisfactory method for sampling active slugs after dark and is not dependent on the skill of the collector to the same extent as in the case of daytime searches.

Certain precautions, such as the avoidance of frosty, windy and excessively dry nights, should be taken in the choice of night on which to sample. If no choice is made, one will in effect be measuring the numbers of slugs active under particular weather conditions and not their activity according to the season. Thus a sample taken in a cold spell or dry period will result in exceedingly small numbers being obtained, although such conditions do not appreciably change the population or that part of the population which would be active under favourable conditions: they merely cause the slugs to become inactive for the time being and the latter will very quickly resume full activity once the conditions alter. This avoidance of obviously unsuitable nights for slug activity reduces appreciably the number of collections necessary to be made in order to obtain a clear indication of the seasonal changes in numbers, which would be masked excessively supposing no account were taken of the conditions prevailing.

The effect of cold, heat and drought on the activity of slugs is dealt with in Part 2, §§ 13 *a*, *d* and *b* respectively. When collecting is done during heavy rain, the numbers of slugs active are markedly lower than when it is not actually raining (see Part 2, § 13 *c*).

Again, when sampling is done during high winds, the number of slugs active is reduced (see Part 2, § 13 *e*). Precautions as to the time of night at which to sample should also be taken, because of the different times of activity according to the season of the year and also of the species (see Part 2, § 12).

Finally, this method of sampling, besides being used to study the seasonal activity of slugs, can also be used in order to obtain data on other slug activities, such as their feeding habits, mating time and breeding season, distribution of species, time of nocturnal activity and the restriction of activity by various weather conditions. All these aspects of their biology and ecology receive attention in Part 2 of this paper.

#### *Presentation of the data*

In such a study as this the data are massive. All are of value, primarily for drawing conclusions, secondarily for suggesting further observation and experimentation, and thirdly, a feature frequently overlooked, in that they enable the conclusions drawn to be checked and, what is just as important, the extraction of further results which may have escaped the attention of the authors.

The data accumulated in the course of this study fall under three headings—half-hour collections, replicated experiments concerning baiting, coring, trapping, etc., and weights.

Besides the various tables designed to bring out special points, tables are given which summarize the full data concerning the half-hour collections. Thus, Tables 5–7 give respectively the total numbers of the species collected after dark in each garden during 1942, in gardens in 1943, and in places other than gardens during 1942; while Tables 11 and 12 give the monthly average numbers per sample after dark in gardens during 1942 and 1943 of the six most common species together with details concerning the number of collections made, the number of gardens visited and the number of nights on which collecting was done.

The full data for every collection since September 1941, when the slugs were first separated into species, are given in the Appendices. The full data for the experiments and weights, however, are not given, but copies are available for inspection in the Entomology and Statistical Departments at Rothamsted Experimental Station.

## 5. ABUNDANCE

### *Arion ater*

*A. ater* was found in 18 out of the 21 gardens visited during 1942 (Table 5) and in 20 out of the 47 gardens visited in 1943 (Table 6). These tables show that it was not equally common in all the gardens. For example, the average numbers collected per sample after dark during 1942 from the back gardens of

Table 5. Numbers of species collected after dark in gardens, 1942

	Arion						Milax				Limax		Total slugs removed	No. of samples	Av. per sample			
	circum- scriptus			hortensis		subfuscus		gracilis		sowerbyi		Agriolimax reticulatus				flavus maximus		
	ater																	
5 Moreton End Lane, back	87	29	4,383	1,158	2,473	362	2,119	0	14	10,625	42	253						
7 " "	62	17	714	271	482	92	950	0	15	2,603	14	186						
9 " "	131	11	497	256	184	429	613	0	10	2,131	12	178						
11 " "	34	3	130	318	121	132	764	0	1	1,503	10	150						
13 " "	114	2	70	280	49	3	517	0	1	1,036	10	104						
15 " "	355	9	79	373	45	3	525	0	16	1,495	12	117						
17 " "	8	0	86	23	11	0	104	0	3	235	2	118						
19 " "	14	0	60	26	65	1	98	0	0	264	2	132						
21 " "	2	3	200	20	90	7	219	0	0	631	3	210						
front	14	19	560	134	414	21	412	0	0	1,574	7	225						
7 " "	25	4	250	120	111	26	341	1	2	880	6	147						
9 " "	0	0	49	10	14	13	133	0	0	219	2	110						
11 " "	7	0	194	57	35	7	283	0	2	585	5	117						
13 " "	32	1	49	89	29	4	342	0	1	547	5	109						
15 " "	63	6	50	99	36	1	282	0	0	537	5	107						
2 Clarence Road	0	0	28	0	0	1	34	0	0	63	1	63						
Vane Lodge, Luton Road	41	0	811	144	297	102	532	0	0	1,927	9	214						
10 Douglas Road	1	1	1,640	76	478	51	677	0	0	2,924	10	292						
Brookfield, Townsend Lane	11	10	363	40	19	1	267	0	2	713	10	71						
Langdale, Salisbury Avenue	1	1	28	1	12	0	46	0	0	89	1	89						
23 Station Road	0	0	125	0	3	0	16	0	1	145	2	73						
Total	1,002	116	10,456	3,495	4,968	1,256	9,274	1	68	30,636	170	—						

Table 6. Numbers of species collected after dark in gardens, 1943

	Arion				Milax			Agrio- limax reticu- latus	Limax		Total slugs removed	No. of samples	Av. per sample
	ater	circum- scriptus	hortensis	subfuscus	gracilis	souverbyi	flavus maximus						
							flavus		maximus				
2 Clarence Road	0	1	5	0	1	60	4	128	2	201	1	201	
4 "	0	0	3	0	2	8	0	95	3	111	1	111	
10 "	0	0	46	0	11	14	0	88	0	159	1	159	
7 Douglas Road	1	0	41	27	15	22	0	84	4	194	2	97	
9 "	0	0	73	21	29	30	0	120	0	273	2	136	
11 "	0	0	5	32	0	8	0	54	0	99	1	99	
13 "	0	0	2	5	1	1	0	71	0	80	1	80	
4 "	0	17	360	35	388	10	0	85	0	885	2	443	
6 "	0	8	441	11	197	4	0	161	0	822	3	274	
8 "	0	2	116	8	54	2	0	34	0	216	1	216	
10 "	1	3	2,116	148	599	79	0	940	0	3,887	13	299	
12 "	0	1	134	7	36	7	0	10	0	195	1	195	
14 "	0	1	164	14	48	55	0	115	0	397	2	199	
16 "	0	0	254	57	70	290	0	172	0	843	4	211	
18 "	0	0	57	30	7	74	0	67	0	236	2	118	
20 "	2	1	75	11	26	6	0	27	0	149	1	149	
22 "	1	1	76	24	291	14	0	98	0	505	2	253	
Moreton End School, Luton Road	1	2	68	153	115	16	0	176	0	532	2	266	
Vane Lodge, Luton Road	5	0	28	38	39	21	0	31	0	162	1	162	
60 Luton Road	0	1	88	0	4	65	0	106	0	264	2	132	
62 "	0	0	4	0	2	16	0	143	0	168	1	168	
64 "	0	0	3	0	1	13	0	82	0	104	1	104	
66 "	0	0	7	0	2	32	0	83	0	125	1	125	
68 "	0	0	15	3	6	59	0	100	0	183	1	183	
70 "	0	0	3	0	1	58	0	124	0	187	1	187	
72 "	0	0	23	0	2	34	0	93	0	154	1	154	
74 "	0	0	11	0	4	27	0	26	1	82	1	82	
76 "	0	0	16	0	1	26	0	13	3	82	1	82	
5 Moreton End Lane	127	58	4,937	2,315	6,398	579	0	2,523	0	16,971	58	293	
7 "	71	4	541	279	506	74	0	801	0	2,285	12	190	
9 "	147	7	448	247	184	262	0	682	0	1,989	13	153	
11 "	33	1	112	308	108	113	0	614	0	1,295	12	108	
13 "	12	0	20	52	24	3	0	60	0	171	2	86	

15 Moreton End Lane	462	9	139	523	62	11	522	0	16	1,744	13	134			
21 "	0	0	107	6	39	0	61	0	0	213	1	213			
29 "	0	0	46	5	3	22	37	0	0	113	1	113			
33 "	4	0	60	18	42	17	82	0	0	223	1	223			
37 "	1	0	17	2	40	9	29	0	1	99	2	50			
41 "	0	0	4	1	3	4	8	0	0	20	1	20			
47 "	2	2	33	0	4	0	18	0	0	59	1	59			
3 Moreton Place	10	0	113	32	61	28	14	0	2	260	1	260			
5 "	43	0	120	58	68	134	147	0	4	574	2	287			
7 "	10	0	6	56	1	17	22	0	2	114	1	114			
4 "	15	2	28	103	25	4	25	1	6	209	1	209			
6 "	19	7	131	46	81	52	95	0	1	432	2	216			
43 Ox Lane	0	1	139	0	45	2	33	0	0	220	2	110			
47 "	0	0	59	4	29	2	36	0	0	130	2	65			
Total	967	129	11,294	4,669	9,675	2,384	9,135	9	154	38,416	181	—			

Table 7. Numbers of species collected after dark in other places, 1942

Vegetable patch at:	Arion						Agrio- limax reticu- latus	Limax <i>flavus maximus</i>	Total slugs removed	No. of samples	Av. per sample	
	ater	circum- scriptus	hortensis	Milax		subfuscus						
				<i>gracilis</i>	<i>sowerbyi</i>							
14 The Pleasance	0	1	191	25	766	7	119	0	0	1,109	5	222
22 Douglas Road	0	0	51	2	36	0	7	0	0	96	1	96
Director's House, West Common	0	5	105	0	29	0	9	0	0	148	1	148
Crouch Hall, Redbourn	4	0	159	1	0	0	127	0	2	293	4	73
24 Douglas Road	2	0	673	3	340	4	71	0	0	1,093	3	364
Potato patch at 5 Moreton End Lane	1	5	241	63	440	31	151	0	1	933	7	133
Allotment: 1	0	6	51	0	12	0	161	0	0	230	1	230
2	3	0	24	0	2	0	185	0	0	214	1	214
3	0	0	57	0	18	0	73	0	0	148	1	148
Field, Harpenden Potato Club	0	0	1	1	0	0	40	0	0	42	1	42
Glasshouse A	0	0	1	0	2	0	11	0	0	14	1	14
Total	10	17	1,554	95	1,645	42	954	0	3	4,320	26	—

Nos. 5, 7, 9, 11, 13 and 15 Moreton End Lane and Brookfield, Townsend Lane, were respectively 2, 4, 11, 3, 11, 30 and 1. In addition, only one specimen was found in ten visits in 1942 and only one in thirteen visits in 1943 to No. 10 Douglas Road. A curious distribution in numbers seemed to exist in Moreton End Lane, progressively more specimens being found as one proceeded up the lane from the Luton Road. This resembled the reverse of what will later be shown to have been the case in certain other species, e.g. *Arion hortensis*.

But in 1943, when more gardens in adjacent roads were visited, this resemblance to a gradient disappeared, and it was seen that there were whole areas of several gardens together where this species was absent or only just present and others where it was more abundant. In fact in one garden, in 1943, 102 individuals were collected in a single sample (see also Part 2, § 11).

*A. ater* also occurred in four of the places other than gardens visited during 1942 (Table 7).

Considering only the gardens, this species came sixth in order of abundance both in 1942 and in 1943, 1002 and 967 individuals respectively having been collected, representing 3% of the total slugs found. However, in some gardens it was relatively more abundant. For example, in 1942 it formed 25% and in 1943 26% of the total slug fauna in the back garden of No. 15 Moreton End Lane.

#### *Arion circumscriptus*

*A. circumscriptus* was found in 14 out of the 21 gardens visited during 1942 (Table 5) and in 20 out of the 47 sampled in 1943 (Table 6). It also occurred in four of the other places visited in 1942 (Table 7). But only 116 specimens were collected from gardens in 1942 and 129 in 1943. So this species was least abundant with the exception of *Limax flavus* and *L. maximus*, forming less than 1% of the total slugs collected. The most found in a single sample has been 17.

#### *Arion hortensis*

*A. hortensis* was found in all the gardens visited in 1942 (Table 5) and in 1943 (Table 6). These tables show, however, that it was by no means equally abundant in each garden. For example, the average numbers collected per sample after dark in 1942 from the back gardens of Nos. 5, 7, 9, 11, 13 and 15 Moreton End Lane and No. 10 Douglas Road were respectively 104, 51, 41, 13, 7 and nearly 7 and 164. A curious and so far inexplicable gradient in numbers has existed throughout 1942 and 1943 in the gardens of the lower six houses in Moreton End Lane. *A. hortensis* has been most numerous in the back garden of No. 5 and has gradually diminished in numbers as one proceeds up the lane until in the back garden of No. 15 it has only just been present. This gradient was not confined to the back gardens but also existed in the front gardens and the gardens

in the neighbouring roads as well. This curious distribution receives full consideration in Part 2, § 11.

Similarly, *hortensis* has been found in all other places visited in Harpenden; the numbers found during 1942 are shown in Table 7.

Considering only the gardens, this species has proved to be the most common one, accounting for 10,546 out of the total of 30,636 slugs collected after dark during 1942 and 11,294 out of the total of 38,416 during 1943. Usually it has been abundant, but there have been gardens where it has been remarkably poorly represented, e.g. some gardens in Moreton End Lane (see above). On the other hand, in several gardens it has been extremely abundant. For example, it has been one of the most numerous in No. 5 and in No. 10 Douglas Road. As further evidence of its abundance it suffices to state that out of the 42 occasions on which samples of slugs were collected after dark during 1942 in the back garden of No. 5, on 20 occasions more than 100 individuals of this species alone were collected during the 30 min. period. On six of these occasions more than 200 specimens were picked up. Further, on the last three occasions when sampling was done in this garden in 1942, 201, 221 and 229 individuals of this species were collected. This seems to indicate rather strongly that frequent sampling, at all events to the extent of 42 half-hour samples and the removal of 4383 individuals spread over a year, does not reduce the numbers able to be collected in a garden of this size. In addition to the slugs removed in after-dark sampling in this garden, many others were removed on other occasions (see Table 4). This applies to all the species. More details as to the numerical abundance of this species are to be found in Appendices 1-3, where it will be seen in two other gardens on four occasions more than 300 individuals were collected during half-hour sampling periods.

#### *Arion subfuscus*

*A. subfuscus* was encountered in 19 out of the 21 gardens visited in 1942 (Table 5), the two gardens in which it was not found being on the east side of Luton Road. In contrast to *hortensis*, which exhibited a remarkable variation in numbers from garden to garden even in the same lane, this species, where it occurs at all, shows a distinct uniformity of distribution, and there is certainly no gradient in numbers in Moreton End Lane. In the back gardens of Nos. 5-15 in this lane averages of 28, 20, 21, 32, 28 and 31 per sample were obtained respectively from the 42, 14, 12, 10, 10 and 12 samples taken during 1942. The front gardens of these properties (ignoring that of No. 9 which was only sampled twice) produced averages of 19, 20, 13, 18 and 20 from 7, 6, 5, 5 and 5 samples. The average number of *A. subfuscus* in samples from gardens in other roads in Harpenden during the same year, while in one case (Vane Lodge, Luton Road) was of the same order (16), in two

other cases (No. 10 Douglas Road and Brookfield; Townsend Lane) was distinctly lower (8 and 4). This may indicate a real difference in abundance.

In 1943 it was found in 34 out of the 47 gardens visited (Table 6). But if one divides the gardens into those on the east and west sides of Luton Road, it will be seen that it occurred in 32 out of the 33 gardens on the west side. In contrast, it was found in only 2 out of the 14 gardens on the east side. This clear-cut presence and virtual absence is the more striking when it is realized that all the gardens on the east side of Luton Road were visited during the period of peak activity of the species. As in 1942 where this species was found at all it occurred almost everywhere in reasonable numbers and no gradients in abundance were noticeable. The absence of this species to the east of Luton Road is further discussed in Part 2, § 11.

*A. subfuscus* was present in most of the other places visited in 1942, but there was a slight indication that it may have been absent from the three allotments (Table 7).

Considering only the gardens, this species during 1942 came fourth in order of abundance, accounting for about 11 % of the total, or 3495 out of the total of 30,636 slugs collected after dark. Considerable numbers have been present in certain gardens as is shown by the fact that in four different gardens (Nos. 5, 11, 13 and 15 Moreton End Lane) over 50 specimens have been picked up in single samples. In these four gardens the highest numbers collected in single samples were 73, 63, 56 and 55 respectively. In 1943 as many as 129 were picked up in a single half-hour collection.

In spite of 13 gardens being visited where this species apparently does not occur, 4669 individuals were collected in 1943. This is 12 % of the total slugs collected and retains fourth place for this species.

#### *Milax gracilis*

*M. gracilis* was found in all except one of the gardens visited in 1942 (Table 5) and in 46 out of the 47 visited in 1943 (Table 6). It probably occurs in every one, but it is by no means equally abundant in each. For example, the average numbers collected per sample in 1942 from the back gardens of Nos. 5, 7, 9, 11, 13 and 15 Moreton End Lane were respectively 59, 34, 15, 12, 5 and 4; while from No. 10 Douglas Road, Vane Lodge, Luton Road and Brookfield, Townsend Lane, the equivalent figures were 48, 33 and 2. In the Moreton End Lane area there is a gradient in abundance which follows that of *A. hortensis* closely (see Part 2, § 11).

Similarly, *gracilis* was found in all except one of the other places visited in Harpenden during 1942 (Table 7).

Considering the gardens only, this species during 1942 came third in order of abundance, accounting for about 16 % of the total or 4986 out of the total of 30,636 slugs collected after dark. This is four times

the number of *Milax sowerbyi* that were collected. 19 out of the 42 occasions on which the ordinary half-hour samples were made after dark during 1942 from the back garden of No. 5 each produced more than 70 specimens of this species; on five of these between 70 and 79, on eight between 80 and 89, on four between 90 and 99 and twice more than 100 (125 and 139). Furthermore, when the area from which the slugs were collected was restricted, e.g. to the vegetable patch, equally large numbers were picked up in the half-hour period (see Appendix 3). Thus, on two occasions more than 100 *gracilis* were collected from the potato patch or hen run at No. 5 and larger numbers still, reaching to 253, were picked up in the vegetable patch at No. 14 The Pleasance. Here *gracilis* was the dominant species from March to May at least, accounting for 62, 69, 68 and 77 % of the population in four samples taken. This tendency to become the dominant species is of particular interest, as this species feeds so largely in the autumn on potato tubers. It may be pointed out here that the whole of the 1941 potato crop at No. 14 The Pleasance was lost by slug attack; this loss must have been largely caused by this species.

In 1943, 9675 individuals of this species were collected. This represents about a quarter of all the slugs captured and was exceeded only by *Arion hortensis*. Considering the numbers collected in single samples, this species heads the list with 371, and out of the 58 samples taken from the back garden of No. 5 two (on the same night) yielded more than 300 each, six 200 or more and 17 over 100. In some of the gardens at least this species appears to have been more numerous in 1943 than in the previous year. In fact in the back garden of No. 5 it was easily the dominant species in 1943, 6398 specimens having been collected compared with the 4937 of the next most abundant species, i.e. *A. hortensis*.

#### *Milax sowerbyi*

*M. sowerbyi* was found in 18 out of the 21 gardens visited in 1942 (Table 5). In 1943 it was encountered in 45 out of the 47 gardens visited (Table 6). It is obvious that it was not equally abundant in all the gardens. For example, average numbers collected per sample in 1942 were nearly 36 in the back garden of No. 9 Moreton End Lane, nearly 7 in the back garden of No. 7, 13 in the back garden of No. 11, 11 at Vane Lodge, Luton Road and 5 in No. 10 Douglas Road. In other gardens it was only just present, thus only one specimen was found in ten visits to Brookfield, Townsend Lane and only three each in ten and twelve samples from Nos. 13 and 15 Moreton End Lane back gardens. The remarkable differences in the numbers in the Moreton End Lane area is commented upon further in Part 2, § 11.

This species was only encountered in three of the other places visited during 1942, namely, the vegetable patches at No. 14 The Pleasance and No. 24

Douglas Road and the potato patch at No. 5 (Table 7).

Considering only the gardens, *sowerbyi* came fifth in order of abundance representing only 4% of the slugs picked up after dark during 1942 and 6% in 1943, 1256 and 2384 individuals respectively having been collected. In Moreton End Lane it was most common in the back garden of No. 9 and in this garden 429 specimens were collected in 1942, which represents 20% of the slug fauna and 262 (or 13%) in 1943. The only other species which were more abundant here were *Agriolimax reticulatus* (613 or 29% in 1942 and 682 or 34% in 1943) and *Arion hortensis* (497 or 23% in 1942 and 448 or 23% in 1943). Even here on only three occasions, all in 1942 (21 September, 100; 1 October, 83; and 14 October, 91) were more than 40 individuals picked up in a single sample. The highest number ever picked up in a single sample in any garden in 1942 and 1943 was 100. Further remarks on the abundance and distribution of this species will be found in Part 2, § 11.

#### *Agriolimax reticulatus*

*A. reticulatus* has been found everywhere both in 1942 (Tables 5 and 7) and in 1943 (Table 6). Reference to these tables shows that, unlike *Arion hortensis*, there was no gradient in numbers as one proceeded up or down Moreton End Lane; the average numbers collected per sample after dark in 1942 being 50, 68, 51, 76, 52 and 44 in the back gardens of Nos. 5-15. The extent to which this species was uniformly distributed can be gauged from the fact that in 19 out of the 21 gardens visited during 1942, the average per sample ranged only from 27 to 76, and of these 19, in 13 it was between 50 and 69 (while for *Arion hortensis* the range for the same gardens was from 7 to 164). The two gardens (No. 2 Clarence Road and No. 23 Station Road) not included in this range were only sampled once and twice respectively, and in these cases the equivalent numbers were 34 and 8.

Considering only the gardens, *reticulatus* came during 1942 an easy second in abundance to *hortensis*, forming 30% of the total slugs collected after dark and 9274 specimens were picked up during the year. In 1943, 9135 individuals were collected, but owing to the increase in numbers of *Milax gracilis* found, *reticulatus* fell into third place. This is one of the many instances which prove that percentage abundance is rather meaningless, since the percentage will vary according to the numbers of other species collected even though the same number of individuals of a particular species may remain constant. With the possible exception of *Arion hortensis* and *Milax gracilis* no two species seem to be dependent on each other directly.

In spite of this numerical abundance and the fact that it has been plentiful in practically all the gardens, the numbers picked up in single samples have not

approached those of *Arion hortensis*, of which in 1942 over 300 individuals have been collected (twice) in one garden, over 200 in two gardens (ten times) and over 100 in nine gardens (38 times). In the case of *reticulatus* the largest number picked up in a single sample during 1942 was 165 (No. 11 Moreton End Lane back garden) and only in seven gardens and on 16 occasions were more than 100 specimens of this species collected in a single sample. In 1943 also the highest numbers per sample of *Arion hortensis* and *Milax gracilis* were not reached by *reticulatus*. In fact, the largest number picked up in a single sample was 163 (and again in No. 11 Moreton End Lane back garden) and only in ten gardens and on 14 occasions were more than 100 picked up in a single sample. This is taken to indicate that the real home of *reticulatus* is not in gardens but in more grassy sites, i.e. fields, etc., whereas that of *Arion hortensis* is, at least nowadays, in cultivated gardens. This is supported by the figures of 185 and 161 *reticulatus* collected in single samples on untidy and semi-deserted allotments (Appendix 3) during March at which season of the year the numbers of this species are usually low. The greatest number collected in gardens during this month was only 74. Full details of the abundance of this species is to be found in Appendices 1-3.

#### *Limax maximus*

*L. maximus* has been found in 12 of the 21 gardens visited during 1942 (Table 5). It formed less than 1% of the slugs collected, only 68 individuals having been encountered. Similarly in 1943 it was found in 25 gardens out of the 47 visited (Table 6), again forming less than 1%, only 154 individuals being collected. But in one garden 23 individuals were found on the one occasion the garden was visited (see Part 2, § 11).

#### *Limax flavus*

Only ten individuals of *L. flavus* have been found throughout the period of this investigation, one in 1942 (Table 5) and nine in 1943 (Table 6). It occurred in five different gardens.

#### Discussion

Throughout this section many statements have been made concerning the number of gardens in which the species have been found, the number of each species collected and sometimes their percentage of the total slugs picked up. It has incidentally already been pointed out that percentage figures do not mean very much, as the different slug species are not, with one possible exception, dependent on each other to any extent. It is worth while considering exactly what such statements mean. Of course the absolute abundance cannot be gauged until a satisfactory method of sampling the basic population has been found. But the relative figures

obtained by the method of sampling by after-dark collecting are worth a little attention.

Two species, e.g. *Agriolimax reticulatus* and *Arion hortensis*, have been found in every garden virtually each time it has been visited, and so they can be said to be very prevalent in the area under consideration. If the gardens visited were to have been chosen completely at random and sampled the same number of times, any species could be stated with some confidence to be the more prevalent, if it had been encountered in more of the gardens and more frequently than another species. On the other hand, although two species, e.g. *hortensis* and *reticulatus*, have been found in an equal number of gardens and just as frequently, *hortensis* has occurred in very large numbers in certain gardens and has been only just present in others, whereas *reticulatus* has been found in considerable numbers in all the gardens. In other words, the numbers of two species found in an area,

several times a month. In order to fill the gaps in the information about the less abundant species, neighbouring gardens were chosen and retained for regular sampling. Here this was done about once a month for the two years, 1942 and 1943. Then, in addition, other gardens in the neighbourhood were sampled occasionally to obtain special information, e.g. about local distribution. But in all cases proximity to the main garden was taken into consideration; one reason for this is obvious when the amount of night work involved is remembered.

In Table 8 the total numbers of each species collected in 1942 and 1943 are shown as well as the greatest number ever collected in a single sample and the number of gardens in which each was found. This table indicates that whereas some species can become exceedingly abundant at times, e.g. *Milax gracilis* and *Arion hortensis*, of which 371 and 315 individuals have been collected in single half-hour

Table 8. Total numbers collected, etc. in Harpenden gardens in 1942 and 1943

Species	Total nos. collected		Greatest no. in a single sample		No. of gardens in which it occurred*	
	1942	1943	1942	1943	1942	1943
<i>Arion hortensis</i>	10,456	11,294	307	315	21	47
<i>Agriolimax reticulatus</i>	9,274	9,135	165	163	21	47
<i>Milax gracilis</i>	4,968	9,675	139	371	20	46
<i>Arion subfuscus</i>	3,495	4,669	73	129	19	34†
<i>Milax sowerbyi</i>	1,256	2,384	100	100	18	45
<i>Arion ater</i>	1,002	967	66	102	18	20
<i>A. circumscriptus</i>	116	129	7	17	14	20
<i>Limax maximus</i>	68	154	7	23	12	25
<i>L. flavus</i>	1	9	1	4	1	4

\* Maximum possible 1942, 21 and 1943, 47.

† In 11 out of 13 gardens lying to the east of Luton Road this species was absent (see Part 2, § 11).

such as the Moreton End district of Harpenden, can be equal and yet their distribution within that area may be quite different. (In the same way the species are localized within gardens.)

Again, one must not compare the abundance of species unless the samples are based on the equivalent points in the curves of their seasonal activity, or, better, on the whole curves. Also the year in which the sampling is done enters into the question, as presumably the populations of the various slugs vary from year to year, independently of each other to a large extent. In gardens especially, the treatment of the area as well as the recentness of such operations (digging, top-dressing, etc.) must also be taken into account in any summation of the slug fauna.

In the present investigation, the gardens were not chosen at random or sampled to the same extent. The back garden of No. 5 formed the initial scene of sampling. Since several species were present in it in reasonable numbers and as cultural operations in it could be controlled, this garden became the main scene of sampling, which was done here

samples, others do not reach such abundance. This is true even when the species has been found in every garden, e.g. *Agriolimax reticulatus*. But since the back garden of No. 5 was sampled so much more often than any other garden (actually this garden was sampled after dark 100 times in the two years and provided 27,596 slugs, while the other gardens taken together were only sampled 251 times and yielded 41,456 slugs), the total numbers of the various species as recorded in Table 8 are biased in its favour. Table 9 shows for comparison the total numbers collected in all the gardens excluding No. 5 back garden. It will be seen that the order of abundance is very similar, but *reticulatus* becomes the most common species. One can therefore assume that such a high proportion of the gardens in the area were visited that the figures of the slugs in all gardens (Table 8) or of those in all except one garden (Table 9) do indicate the comparative abundance of the species in the area as measured by after-dark collecting; and, in addition, that the back garden of No. 5 was typical of the district.

The numbers collected in the two years are, however, influenced by the fact that the fauna in different gardens is not the same, and that the same gardens were not in all cases sampled during both years. This is notably so in the cases of *Milax sowerbyi* and *Limax maximus*, of which greater numbers were found in more gardens that were sampled during 1943 than during 1942. The question of the distribution of the species from garden to garden is deferred until Part 2, § 11, but the abundance of the species from year to year is worth considering briefly.

Table 10 collects the information available about the numbers found per sample in each garden that has been sampled regularly (i.e. ten or more times) throughout each of the two years 1942 and 1943. There were definitely more *Milax gracilis* in the back garden of No. 5 during 1943 than in 1942. There were probably more *Arion subfuscus* and probably fewer *A. hortensis*. On the other hand, the numbers

Table 9. Total numbers collected in all gardens except No. 5 Moreton End Lane back garden

	1942	1943
<i>Agriolimax reticulatus</i>	7155	6612
<i>Arion hortensis</i>	6073	6357
<i>Milax gracilis</i>	2495	3277
<i>Arion subfuscus</i>	2337	2354
<i>Milax sowerbyi</i>	894	1805
<i>Arion ater</i>	915	840
<i>A. circumscriptus</i>	87	71
<i>Limax maximus</i>	54	120
<i>L. flavus</i>	1	9

of *A. ater*, *Milax sowerbyi* and *Agriolimax reticulatus* showed no change. Regarding the numbers in the other gardens it is not possible to draw any conclusions owing to the small number of samples, combined with the extent of the seasonal range in numbers of the various species. Considering the total slug population of the gardens, the increase shown in the back garden of No. 5 can be ascribed to the increase in *Milax gracilis*. In contrast, the reduction at Nos. 9 and 11 Moreton End Lane could be due to the presence of ducks on free range and to rather drastic cultivation at intervals respectively. The increase at No. 15 Moreton End Lane may be due to a real increase of *Arion subfuscus*. This species showed a tendency to be rather more common in several gardens in 1943 than in 1942.

## 6. SEASONAL ACTIVITY

### *Arion ater*

Unfortunately, in the back garden of No. 5, where most samples were taken, this species is not abundant, and so it is not possible to trace the seasonal abundance or activity of this species in this garden. But using the data obtained less frequently in other

gardens, it has become apparent that most *ater* are usually to be found in January. Taking advantage of our initial mistake in considering the young straw-coloured specimens of *ater* to be a distinct species, it has been our practice to keep separate records of the occurrence of the young and smaller individuals from those of the larger and older specimens. It is obvious that the peak of abundance in the back garden of No. 15 Moreton End Lane occurred in 1942 in January and consisted of the young ones, while the large individuals reach a peak in August to September. This agrees with what was found to occur in other gardens (see Appendices 1 and 2).

In 1943 the same general trend of the young ones to be most numerous at the beginning and end of the year was noticeable. But more half-grown ones and nearly full-grown ones were found during April–June and in this latter month the actual peak number for the year was collected. It seems that the mild winter and spring may have resulted in more young surviving and growth being more rapid.

The average numbers per sample in gardens from month to month in 1942 are given in Table 11 and the corresponding figures for 1943 are shown in Table 12. The seasonal trend in numbers is masked to a large extent owing to the fact that in only one garden have there been any considerable numbers of *ater*.

### *Arion circumscriptus*

Owing to the paucity of the data it is not possible to draw any conclusions as to this species' seasonal activity. It may prove to be more active and numerous between October and May (cf. *A. hortensis*) than during the rest of the year (cf. *Limax maximus*) (for details see Appendices 1 and 2).

### *Arion hortensis*

In spite of *hortensis* being such an abundant species, the numbers collected on favourable nights for activity have varied considerably according to the season of the year. The numbers of this species collected per sample after dark in the back garden of No. 5 are given in the form of a graph in Fig. 3.\* It will be seen that there was a steady rise in the numbers collected from October to December 1941. This was followed by a great reduction in numbers active during the cold period at the beginning of 1942. Immediately after the warm weather started there was a sudden rise in numbers, only to be followed by a sharp reduction during the drought period in April and May. As soon as the drought broke there was another immediate rise in numbers which in its turn was brought to nil during the hot

\* The results obtained in one pre-dawn sampling between 03.00 and 03.30 hr. on 13 April have been omitted from the graphs throughout this paper, since this was an exceptional time of sampling.



and dry weather in June. In this instance, however, when the weather broke there was not that equally sudden return to large numbers being active which was observed immediately following the end of the

less, when the numbers did eventually regain their previous level in August, they remained about level until after the rainless period in the first three weeks of September. Then for the rest of 1942

Table 12. Monthly average numbers per sample after dark in gardens, 1943

	Arion			Milax		Agrio- limax reticu- latus	All species (9)	No. of samples	No. of dates on which sampling was done	No. of gardens visited (47)
	ater	hortensis	subfuscus	gracilis	sowerbyi					
Jan.	10	107	22	34	5	42	220	16	10	6
Feb.	4	78	19	34	3	36	174	10	6	6
Mar.	8	72	20	36	7	31	175	10	8	6
Apr.	10	80	36	54	9	30	221	12	9	8
May	7	48	46	41	16	32	192	29	18	25
June	7	13	40*	23	19	85	190	22	13	18
July	5	14	37	29	8	78	172	14	9	10
Aug.	3	35	27	62	21	80	229	11	7	7
Sept.	2	87	15	87	18	66	275	12	10	8
Oct.	1	87	6	94	17	47	252	31	18	24
Nov.	3	90	9	79	10	35	226	9	7	6
Dec.	6	66	11	69	4	25	186	5	4	3
								181	119	

\* The average is 79 if one excludes 11 gardens to the east of Luton Road where this species is virtually absent. In all other months sampling was restricted to gardens on the west side of this road.

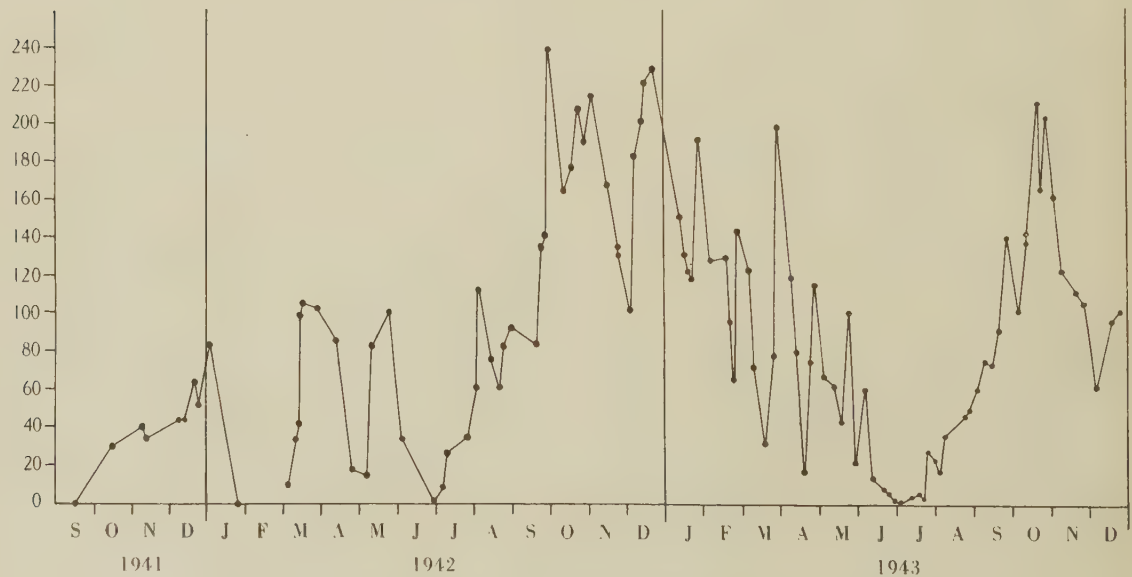


Fig. 3. Seasonal activity of *Arion hortensis* in No. 5 Moreton End Lane back garden, 1941-3.

cold weather early in the year and again following the break of the April-May drought. This slower return to full activity may have been due to the fact that more rain is required to wet the soil thoroughly in July than in May or it may be that there was actually some mortality among the slugs. Neverthe-

much larger numbers of this species were active (collected) than had been observed previously. The exceptionally high number (239) collected on 30 September, following the two previous nights when much lower numbers (135 and 141) have been found, cannot be explained. Neither can the reduction from

about the 200 level on 3 November to 168 on 15 November and 131 and 135 on 25 November. The lowest number (102) on 5 December, on the other hand, can be attributed to the windy condition prevailing on that night. Such inexplicable fluctuations serve to show that it is extremely difficult to select the nights of maximum activity.

In January 1943 the numbers of slugs on what were considered to be suitable slug nights showed a marked reduction from the December level. At the end of the month (28 January) the number found active once more rose to about the 200 level that was typical of the last quarter of 1942. It also did so again on one night in March. But, taken as a whole, the numbers steadily decreased from the beginning of 1943 until the trough in numbers found active was once again reached in June and July. It may be that the fall in numbers really starts in November and that the large numbers found in December 1942 were exceptional and due to the unusually mild weather. After the 1943 trough the numbers rose again until the peak was reached during October. The steadiness of this 1943 autumnal rise is in striking contrast with the irregularities exhibited in the decline during the first half of the year. Supposing the nights on which the highest numbers were collected are taken to represent the most favourable nights for activity and those on which the lowest numbers were collected are the most unfavourable, it would be expected that a similar inexactitude by the collector in choosing nights of equal favourableness for slug activity would be exhibited throughout the year. But the curve for August and September is much more regular than that in the earlier part of the year. This can be explained if there is a real increase in the absolute population and if at the same time the increase is so rapid that the number of slugs active on an unfavourable night a few days after a favourable one is greater than on the previous favourable night, in spite of a lower percentage of the actual population being active.

The steadiness of this autumnal rise in 1943 is also different superficially from that in 1942. But in this latter year there was a three-week period without rain in September and there had not been sufficient rain in August to wet thoroughly the ground following the normal drying out of the soil during the summer. In 1943, on the other hand, the moisture conditions seemed to be completely favourable for slug activity throughout the autumn. The 1943 peak numbers were reached in October and then a drop was observed in November and December. This follows what happened in 1942 except that there was not the recovery to really large numbers in December. This lends support to the view expressed above that the seasonal fall in numbers of this species is slow and extends over 8-9 months (November until June and July the following year) and is followed by a quick big rise lasting only about three months, reaching its

peak in October. This basic pattern will, of course, be slightly modified each year owing to seasonal differences in the weather.

It has already been mentioned that the numbers of this species were probably lower in this garden during 1943 than in the previous year, but more striking is the difference in the distribution of their activity within the year. In 1943 there were large numbers active in both halves of the year, 2570 being collected during January-June and 2367 from July to December. In 1942, on the other hand, four times as many *hortensis* were collected in the second half of the year as in the first half. This difference in activity is obviously due to the weather. The importance of such differences in seasonal activity in relation to damage is pointed out later (Part 2, § 10e).

The rise observed during the last four months in 1941, although significant, was probably chiefly due to the lack of experienced and proper sampling during September and October.

The rather pronounced susceptibility of this species to isolated unfavourable nights for activity, in spite of the apparent increase in numbers during the winter months, should be noted, as well as the usually quick recovery to full activity as soon as the conditions change.

Fig. 4 shows that the same general trends, particularly the autumnal increase in numbers, have existed in other Harpenden gardens. This was irrespective of whether there were large or small numbers of *hortensis* present in the gardens. Comparable figures for still further gardens can be found in Appendix 2.

The average numbers per sample in all gardens from month to month in 1942 are given in Table 11 and the corresponding figures for 1943 are shown in Table 12. Fig. 5 illustrates these seasonal trends in activity as exhibited by *hortensis* in the back garden of No. 5.

#### *Arion subfuscus*

The seasonal activity curve of *subfuscus* has been essentially one of increased activity in May, June, July and August, almost entirely composed in these months of large and apparently mature individuals (see Part 2, § 9), with a marked reduction during the winter and early spring months. The numbers of this species collected per sample after dark (see footnote on p. 160) in the back garden of No. 5 are given in the form of a graph in Fig. 6. It will be seen that the cold spell at the beginning of 1942 did not reduce very much the already small numbers which were active at the end of 1941. There appears to have been a definite beginning of an increase in the numbers active, and so collected, just before the drought period in April and May, but this tendency was checked temporarily by the dry weather. After rain had fallen this increase in activity was established until the hot dry weather at the end of June and beginning of July. Then at the end of July and

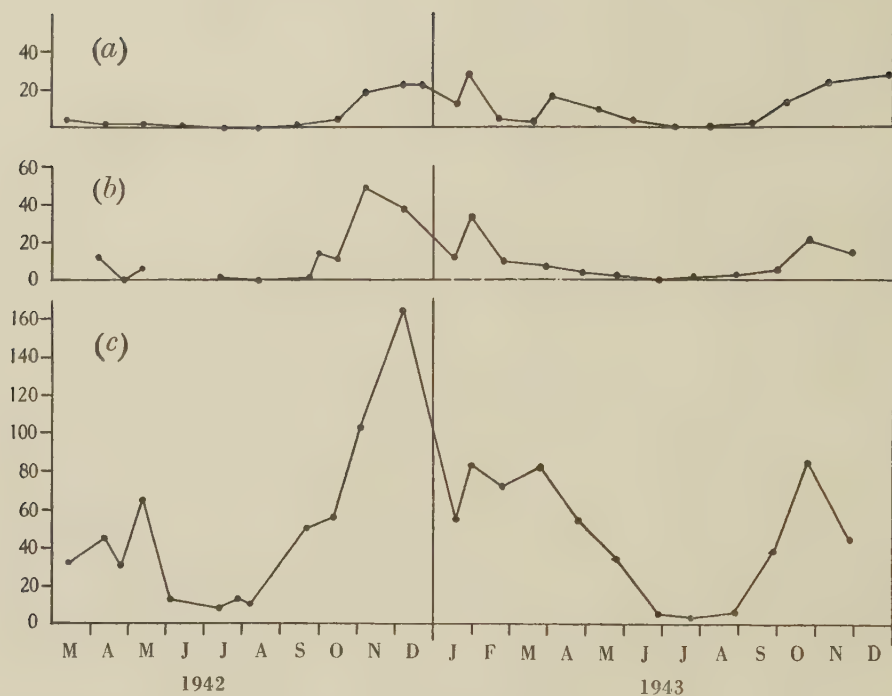


Fig. 4. Seasonal activity of *Arion hortensis* in other Harpenden gardens, 1942-3; in the back gardens of (a) No. 15, (b) No. 11 and (c) No. 7 Moreton End Lane.

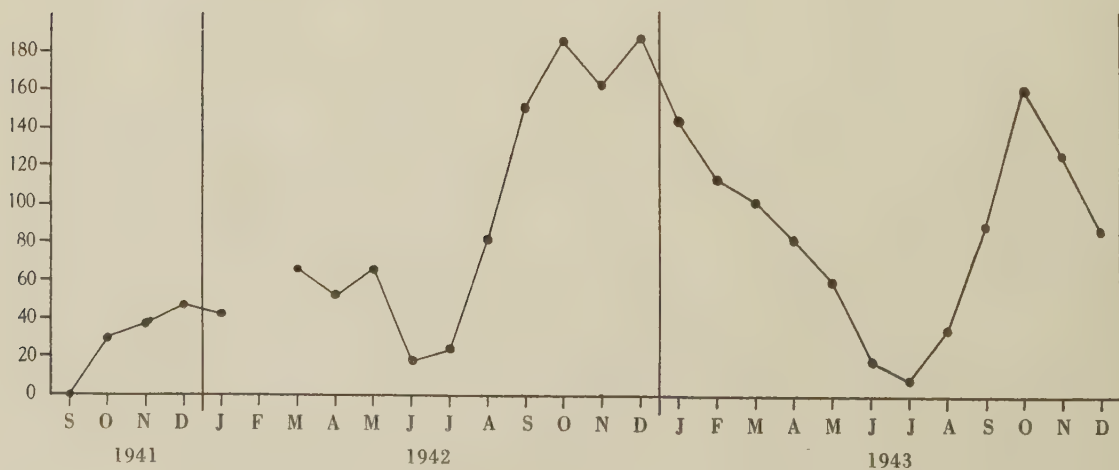


Fig. 5. Average monthly activity of *Arion hortensis* in No. 5 Moreton End Lane back garden, 1941-3.

beginning of August the numbers regained their previous high level, but later in the latter month the numbers started to fall. This decline in numbers active continued until, at the end of November and the beginning of December 1942, the numbers found were the same as at the end of 1941. Towards the end of December and early in 1943 there were indications of increased numbers being active. This increase was due to the appearance of considerable numbers of newly or recently hatched individuals. The summer increase in numbers was again obvious and well defined. But the peak was reached earlier, i.e. in May–June. One consequence of this was that, although the numbers found active in July were irregular, there was not a return to peak numbers in

activity as exhibited by this species in the back garden of No. 5. It will be seen that the summer increase in numbers found active after dark is very pronounced and must be considered an established fact.

It should be noted in passing that the average number of *subfuscus* picked up per sample after dark in gardens was the same at the beginning and end of 1942 and 1943, in spite of greatly increased numbers being active each summer and the peaks being at different heights in the two years. This is true whether the gardens are considered separately or together and may be taken to show that the population of *subfuscus* did not increase during 1942 nor in 1943.

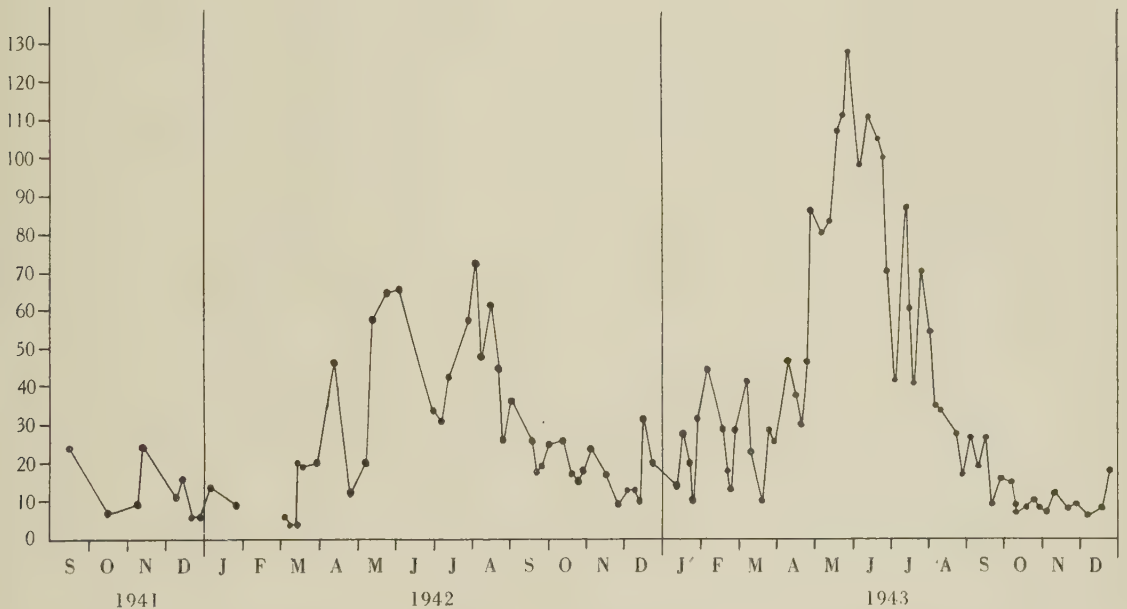


Fig. 6. Seasonal activity of *Arion subfuscus* in No. 5 Moreton End Lane back garden, 1941–3.

August as there had been in 1942. In fact by August the numbers had returned to a low level. The fewest individuals were active during October, November and early December and then the increased presence of young ones again was beginning to make itself felt.

It will be noticed by comparing Fig. 6 with Fig. 3 that *subfuscus* does not appear to react so violently to isolated unfavourable nights for activity as does *Arion hortensis*.

Fig. 7 shows that the same general trends have existed in other Harpenden gardens. Comparable figures for other gardens can be found in Appendix 2.

The average numbers per sample in all gardens from month to month in 1942 are given in Table 11 and the corresponding figures in 1943 are shown in Table 12. Fig. 8 illustrates these seasonal trends in

#### *Milax gracilis*

The seasonal activity curve of *gracilis* resembles that of *Arion hortensis*. The numbers of this species collected per sample after dark (see footnote on p. 160) in the back garden of No. 5 are given in the form of a graph in Fig. 9. It will be seen that the cold spell at the beginning of 1942 affected the activity of this species just as severely as it did that of *hortensis*. Again, there was a rise in numbers active soon after the cold spell had stopped, the numbers regaining their former level, but not so suddenly as did those of *hortensis*. This level of numbers was maintained until the drought period at the end of April but there seems to have been a definite increase in May and June. The hot dry weather in June seems to have had less effect in this particular garden on this species

than on *hortensis*. In fact the general level of activity seems to have remained about the same from May until late September. Then in late September and in October there was a period when greater numbers

In January 1943 the numbers found active were slightly less on the average (*c.* 63). The numbers in February, March and April were exceedingly variable but on the average reached their lowest point in

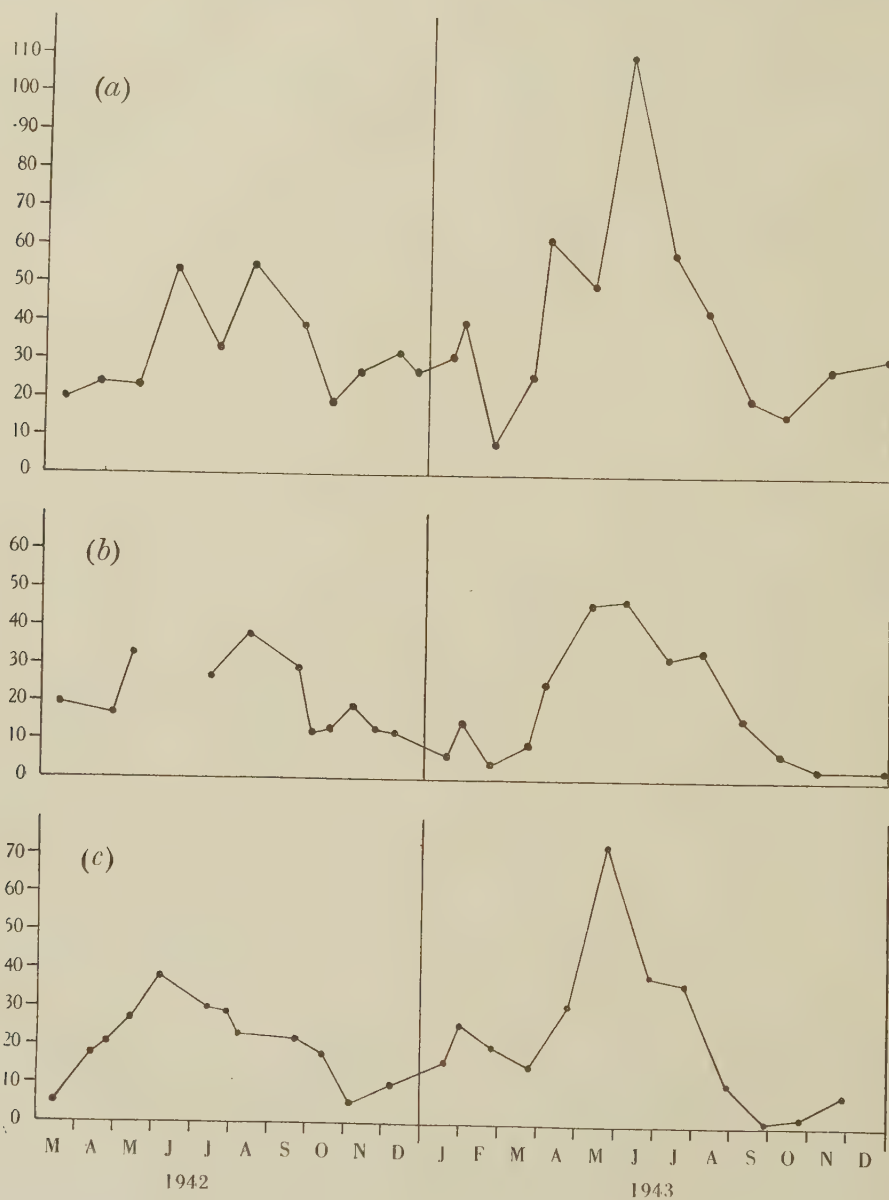


Fig. 7. Seasonal activity of *Arion subfuscus* in other Harpenden gardens, 1942-3; in the back gardens of (a) No. 15, (b) No. 9 and (c) No. 7 Moreton End Lane.

were active followed by a return to the August level (*c.* 75) which was maintained (*c.* 80) from the end of October until the end of the year. The lowest number (32) on 5 December can be attributed to the windy conditions prevailing on that particular night,

February and March, while in April on the average they started to rise. In May this level was again increased. The numbers then fell in June and July. But in August the May figures were again reached. In September there was another rise followed by a

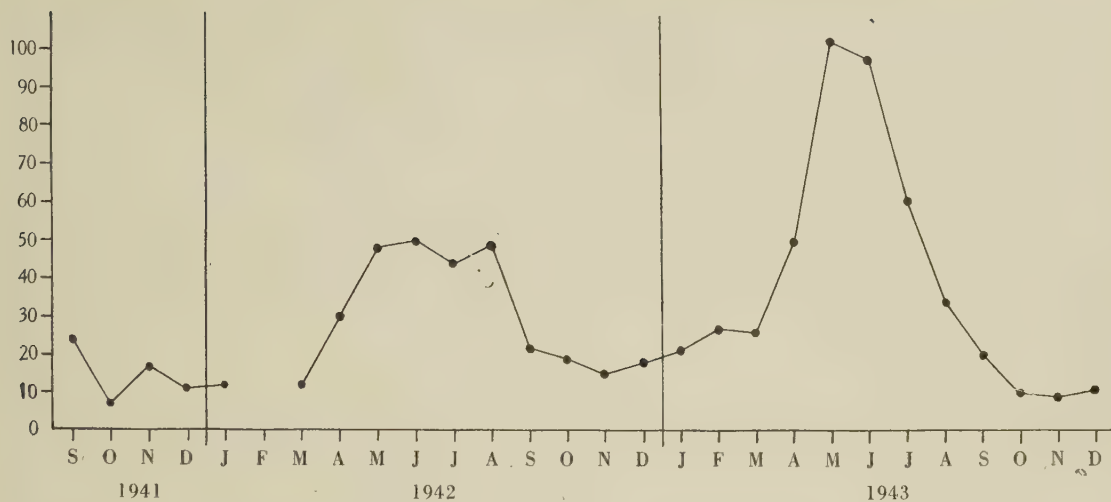


Fig. 8. Average monthly activity of *Arion subfuscus* in No. 5 Moreton End Lane back garden, 1941-3.

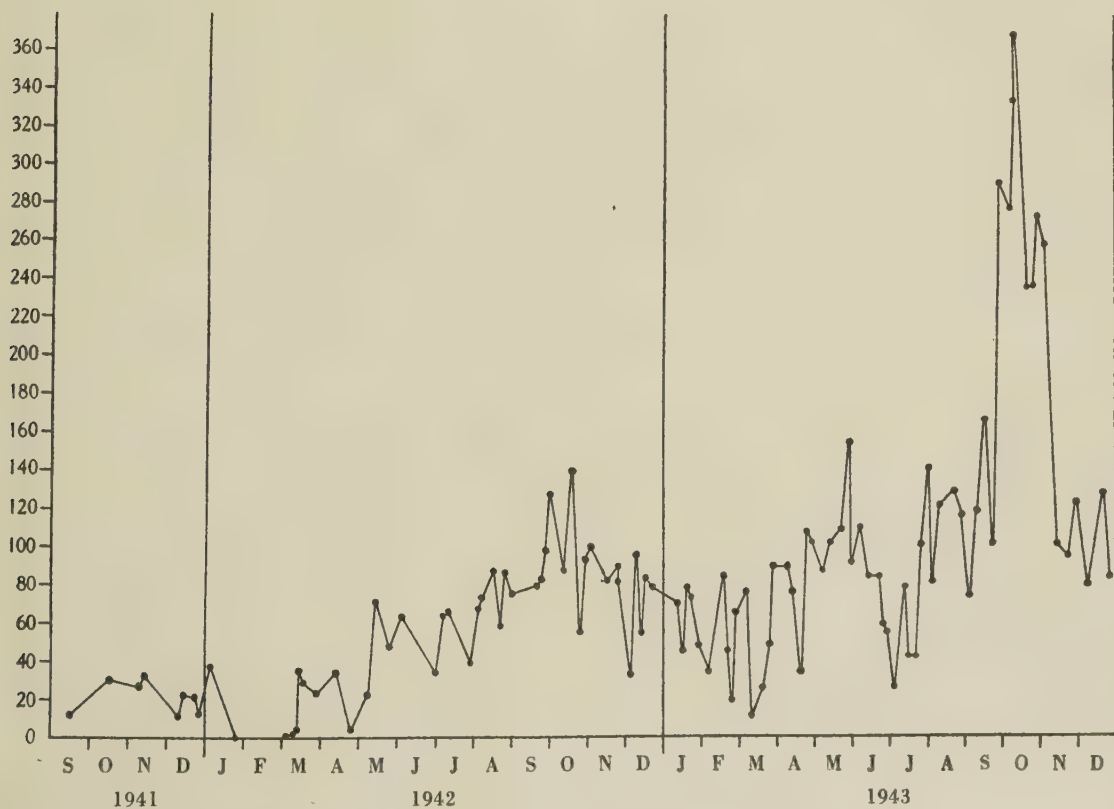


Fig. 9. Seasonal activity of *Milax gracilis* in No. 5 Moreton End Lane back garden, 1941-3.

huge increase in October when the average of six samples on five different nights was 290, a figure which is more than 100 greater than the highest monthly average number for this or any other species. In November and December the numbers fell to about the August and September levels.

The return to full activity after winter cold should be noticed. This is less rapid than in the case of *Arion hortensis* and may be due to the greater depth to which *Milax gracilis* retires in cold weather.

Fig. 10 shows that the same general trend towards an increase in the autumn and winter, as well as the effect of the cold and drought, have existed in other

after dark (see footnote, p. 160) in the back garden of No. 5 are given in graph form in Fig. 12. In spite of the fact that the figures are low, it will be seen that here activity stopped in the cold spell early in 1942, that a reduction took place in the spring drought and possibly there was another reduction in the warm weather in July. In August, however, the numbers rose definitely and remained comparatively high until 17 October. The actual peak was on 31 August when 30 individuals were collected. From the end of October 1942 until the end of the year the numbers were again low, single figures on practically each occasion.

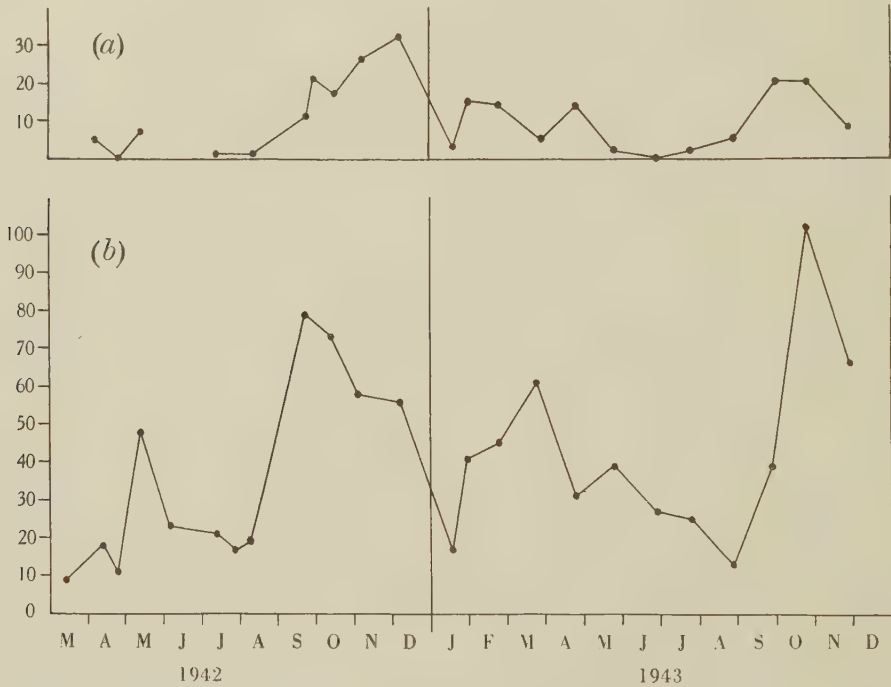


Fig. 10. Seasonal activity of *Milax gracilis* in other Harpenden gardens, 1942-3; in the back gardens of (a) No. 11 and (b) No. 7 Moreton End Lane.

Harpenden gardens. Data for still other gardens are given in Appendix 2.

The average numbers per sample in gardens from month to month in 1942 are given in Table 11 and the corresponding figures for 1943 are shown in Table 12. Fig. 11 illustrates these seasonal trends in activity as exhibited by *gracilis* in the back garden of No. 5. It will be seen that on the average there was a period of reduced activity in July.

#### *Milax sowerbyi*

In spite of the rather low numbers of abundance it is quite obvious that *sowerbyi* reaches a peak period of activity in the late summer and early autumn. The numbers of this species collected per sample

In 1943, after a trough of low numbers in February, there was a tendency for the numbers to increase, particularly in May. After this there was a slight falling off in numbers during June and July. But in August there was again a definite rise reaching the peak for the year in late September and early October. Then there was a fall and from mid-November onwards there was a very marked reduction in the numbers found per sample.

Fig. 13 shows that the same general trends have existed in other Harpenden gardens. Comparable figures for other gardens can be found in Appendix 2.

The average numbers per sample in gardens from month to month in 1942 are given in Table 11 and the corresponding figures for 1943 are given in

Table 12. Fig. 14 illustrates these seasonal trends in activity as exhibited by this species in the back garden of No. 5. It may be accepted as established that *sowerbyi* shows a well-defined increase in activity during August, September and October with the peak about September.

trough was reached in December and continued until the end of March. The cold spell early in 1942 scarcely affected this species, that is to say that whenever sampling was done during this period no appreciable reduction in the number of specimens found active was noticeable. (It is understood, of course,

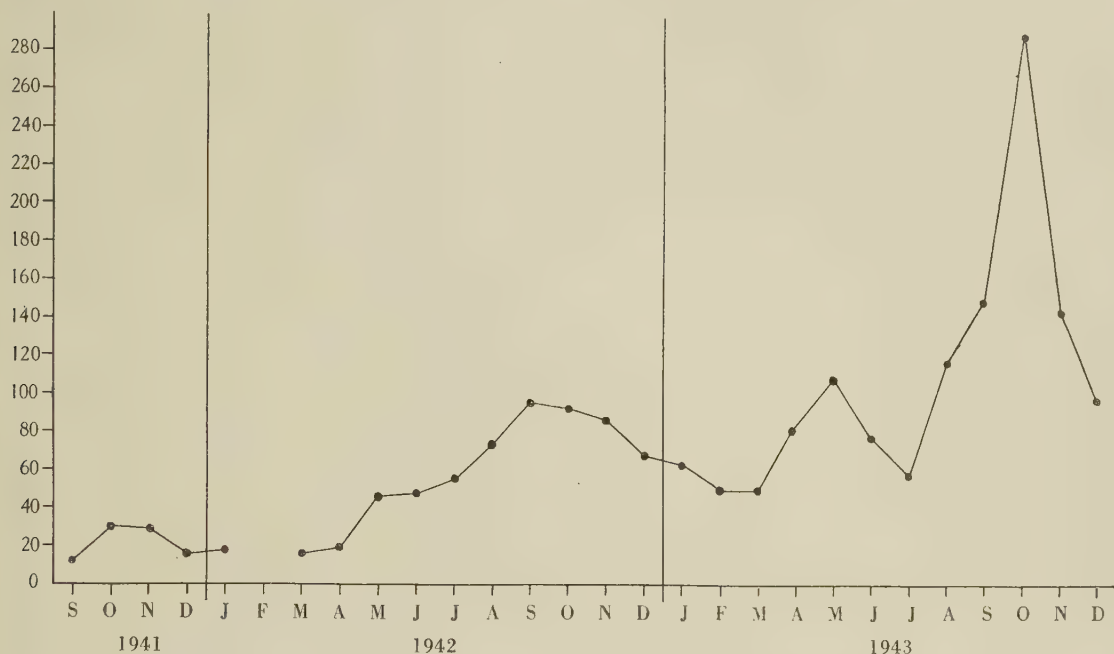


Fig. 11. Average monthly activity of *Milax gracilis* in No. 5 Moreton End Lane back garden, 1941-3.

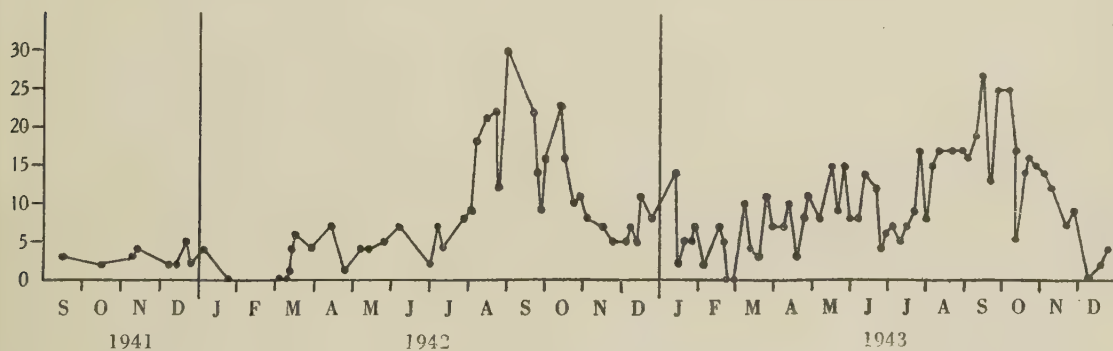


Fig. 12. Seasonal activity of *Milax sowerbyi* in No. 5 Moreton End Lane back garden, 1941-3.

#### *Agriolimax reticulatus*

The seasonal activity of *reticulatus* is most interesting. The numbers of this species collected per sample after dark in the back garden of No. 5 are given in the form of a graph in Fig. 15 (see footnote, p. 160).

It will be seen that the high numbers active in September 1941 fell rapidly to a low level whose

that no activity takes place when the temperature is below freezing point.) This is quite different from what happened in the cases of *Arion hortensis* (Fig. 3), *Milax gracilis* (Fig. 9) and *M. sowerbyi* (Fig. 12), but not dissimilar to what happened in the case of *Arion subfuscus* (Fig. 6). After the cold spell there was a tendency for a rise in the numbers active, but the dry period at the end of April and in May reduced the

numbers active again. Likewise at the end of May and in June there was a tendency for an increase, after which the numbers were again reduced to the winter level at the end of June and beginning of July. But in late July a definite increase in numbers took place and this increased steadily until the greatest

In 1943 this trough was continued until June and there was no tendency for an increase in numbers during April and May as there had been in 1942. But the numbers increased more or less steadily throughout June and July until the peak was reached in late July and early August. This was about a month

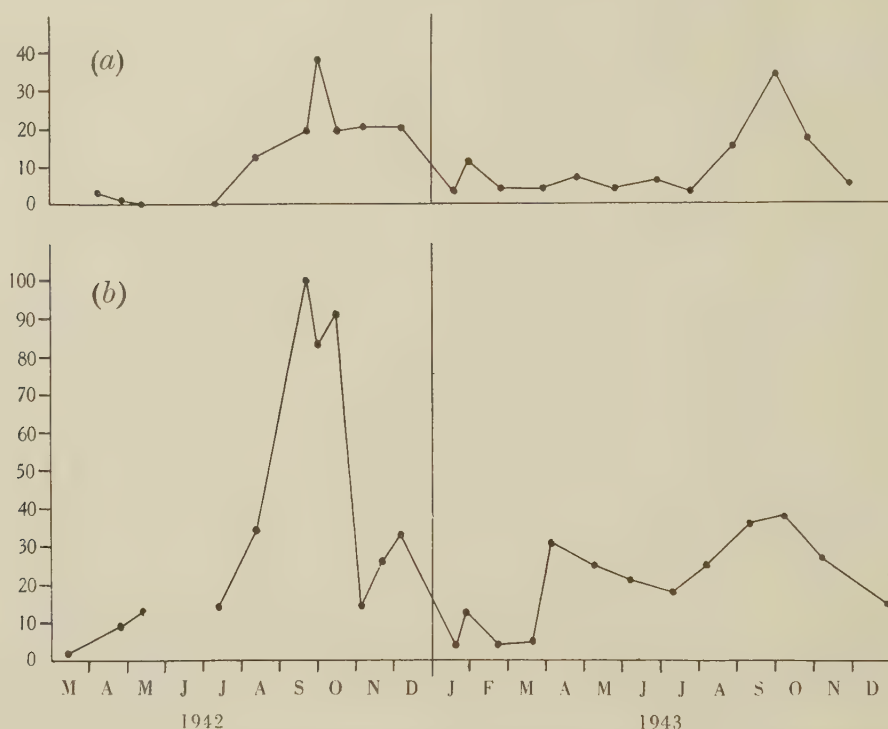


Fig. 13. Seasonal activity of *Milax sowerbyi* in other Harpenden gardens, 1942-3; in the back gardens of (a) No. 11 and (b) No. 9 Moreton End Lane.

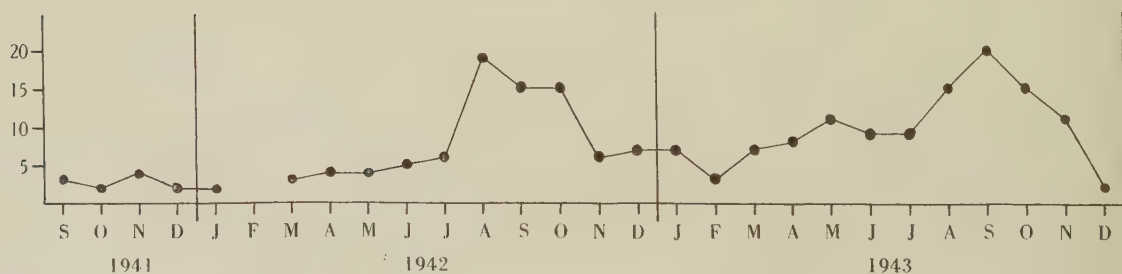


Fig. 14. Average monthly activity of *Milax sowerbyi* in No. 5 Moreton End Lane back garden, 1941-3.

numbers were found active on 31 August and 20 September. Actually there was no rain during the first part of September, otherwise it is possible that the 1941 peak (155) would have been reached or surpassed. After 20 September the numbers fell rapidly to a low level whose trough was reached in late November and early December.

earlier than in the previous year and may have been due to the fact that there was no check in July as there had been in 1942. In August the numbers started to fall and the trough was reached in December.

The general lack of response shown by *reticulatus* to adverse weather conditions and general appearance of a fixed rhythm should be compared with that of

*Arion subfuscus* and is in direct contrast to the great fluctuations in activity exhibited by such other species as *A. hortensis* and *Milax gracilis*.

Fig. 16 shows that the same general trends have existed in other Harpenden gardens. Comparable figures for still other gardens can be found in Appendix 2.

The average numbers per sample in gardens from month to month in 1942 are given in Table 11 and the corresponding figures for 1943 are shown in Table 12. Fig. 17 illustrates these seasonal trends in activity as exhibited in the back garden of No. 5.

### Discussion

The evidence in this section establishes the fact that the different species reach their peaks of numerical nocturnal activity at different seasons of the year. Fig. 18 condenses this information concerning five species and is based on the average monthly figures obtained by after-dark collecting in five different gardens. It has already been pointed out (Barnes, 1944) that the same trends of the species' seasonal activity have been obtained whether the curves are based on the data of collections in one garden frequently (No. 5 Moreton End Lane) or in

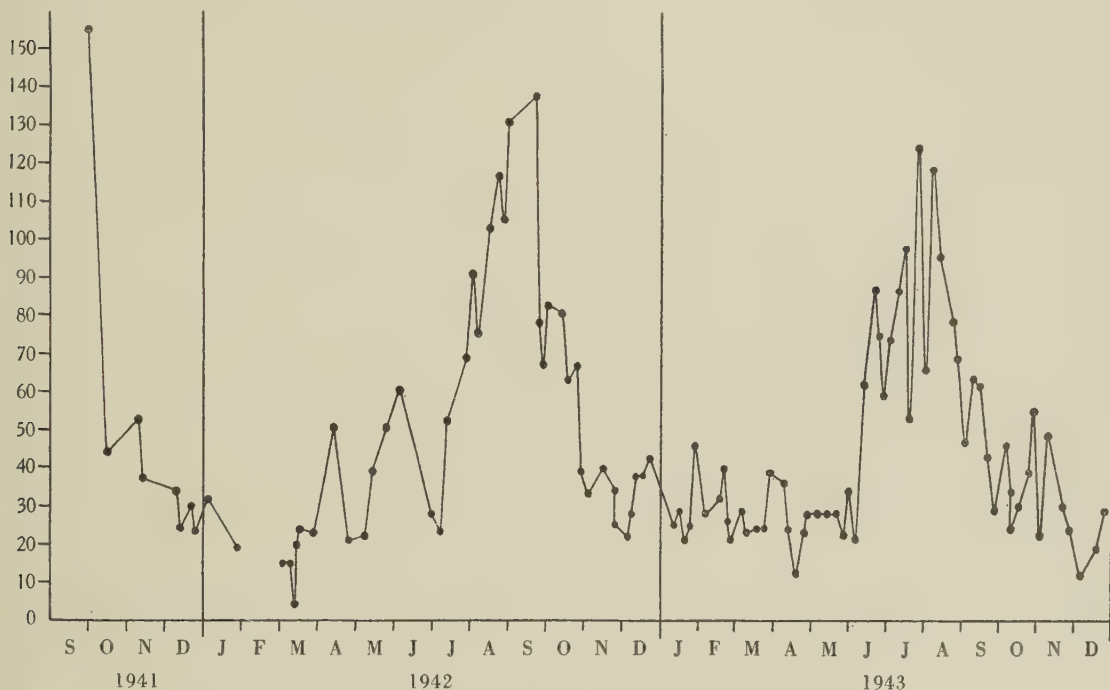


Fig. 15. Seasonal activity of *Agriolimax reticulatus* in No. 5 Moreton End Lane back garden, 1941-3.

It may be noted that on the average the number of *reticulatus* picked up at the beginning and end of 1941, 1942 and 1943 was about the same.

### *Limax maximus*

Owing to the infrequency with which this species has been met, no conclusions can be drawn as to its seasonal activity. It does seem, however, that more and larger specimens are active during the summer months, while fewer and smaller individuals are active during the winter (contrast *Arion circumscriptus*, p. 160). What little information has been obtained on this point is contained in Appendices 1 and 2.

### *Limax flavus*

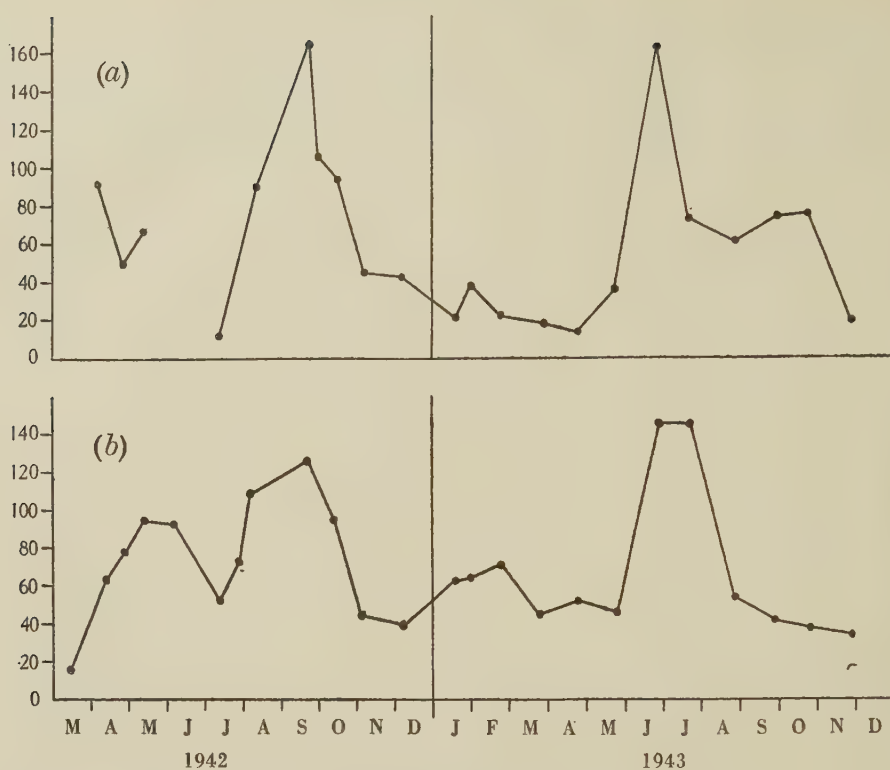
Too few specimens of *L. flavus* have been encountered to warrant any statement concerning its seasonal activity.

other individual gardens at intervals of approximately a month. Averages of the data obtained by sampling one garden frequently or a group of five different gardens or the total number of gardens sampled likewise exhibit the same general trends. These trends are obvious whether there are small or large numbers of the species present in particular gardens.

Consequently it appears that in any ordinary garden one can expect a succession of peaks in numerical abundance of active slugs throughout the year, starting with *Arion ater* very early, followed by *A. subfuscus* and probably *Limax maximus* in the drier summer months, while *Agriolimax reticulatus*, *Milax sowerbyi*, *M. gracilis* (at potato harvest time) and *Arion hortensis* follow each other in rapid succession throughout the autumn and on to the New Year.

If, however, one compares the data derived from

## Slugs in gardens



[Fig. 16. Seasonal activity of *Agriolimax reticulatus* in other Harpenden gardens, 1942-3; in the back gardens of (a) No. 11 and (b) No. 7 Moreton End Lane.

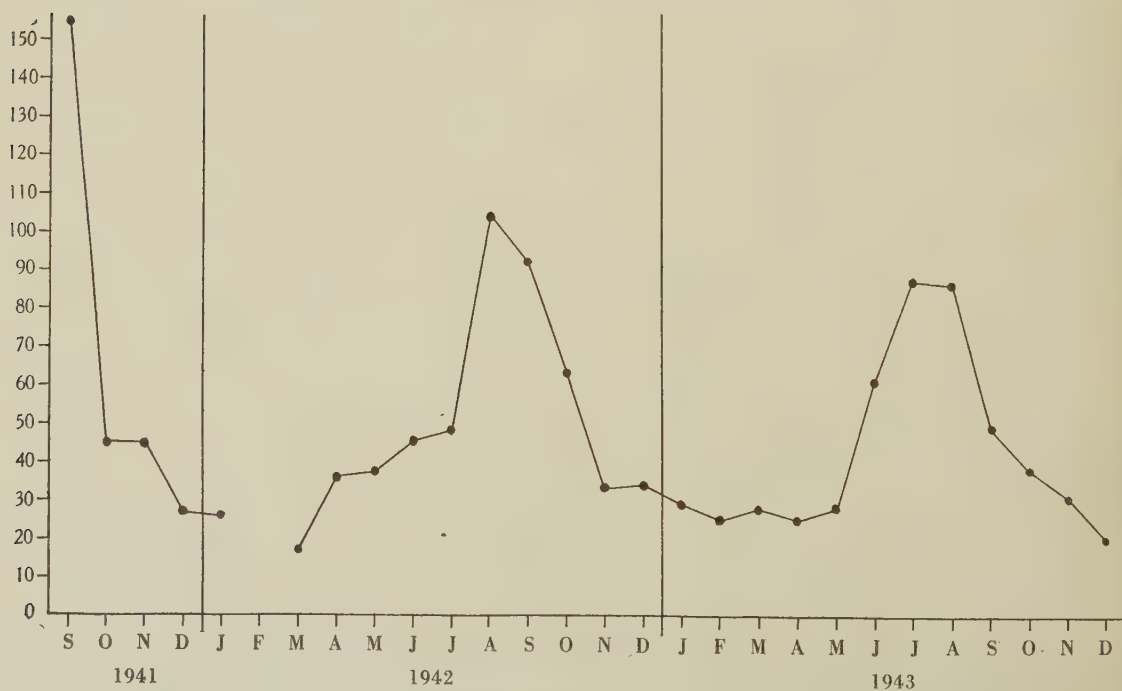


Fig. 17. Average monthly activity of *Agriolimax reticulatus* in No. 5 Moreton End Lane back garden, 1941-3.

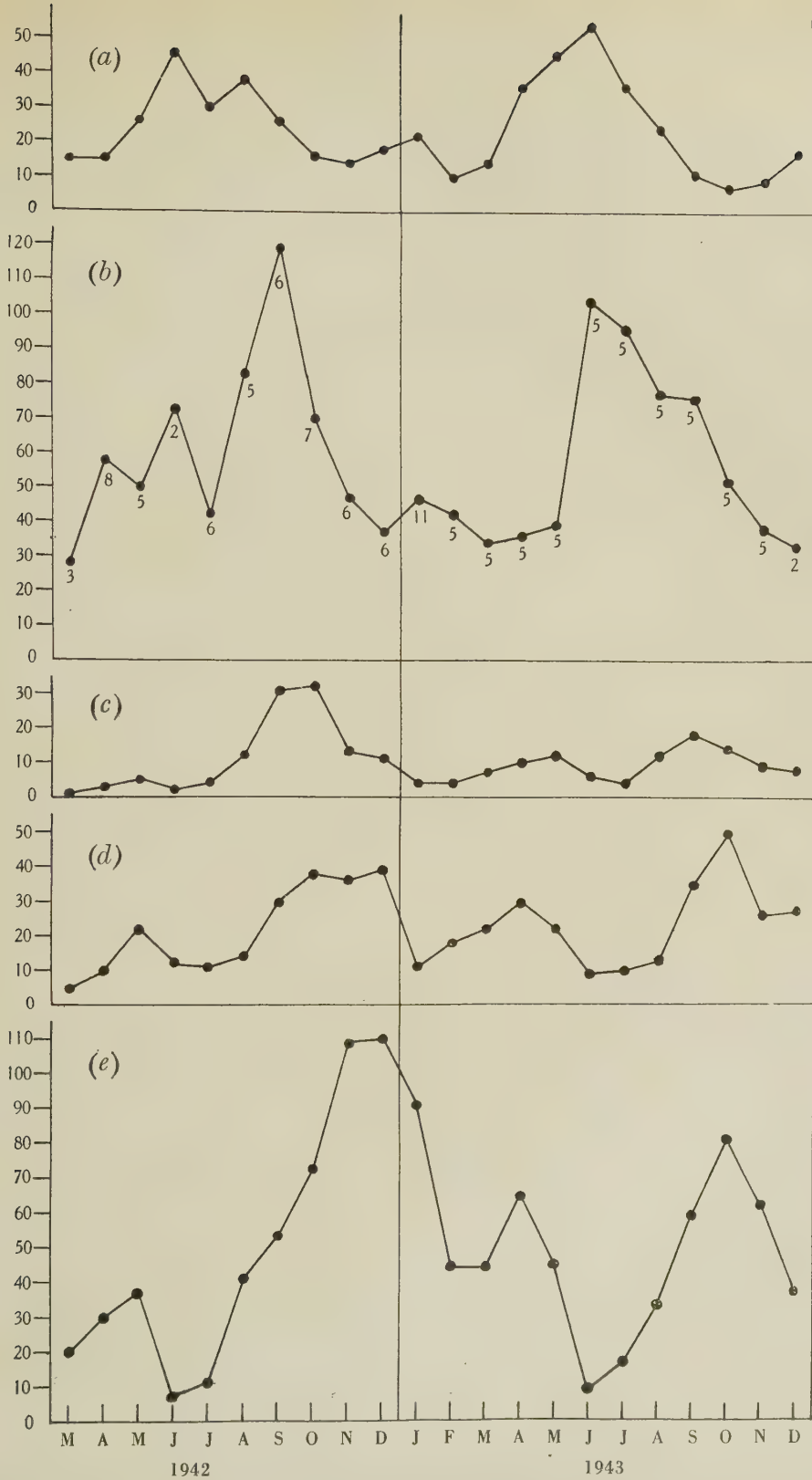


Fig. 18. Average monthly activity of (a) *Arion subfuscus*, (b) *Agriolimax reticulatus*, (c) *Milax sowerbyi*, (d) *Milax gracilis* and (e) *Arion hortensis* in five Harpenden gardens. The gardens, in each case the back garden, are those of No. 10 Douglas Road and Nos. 7, 9, 11 and 15 Moreton End Lane. The figures in (b) indicate the numbers of collections from which the monthly averages have been obtained.

individual gardens, there is evidence (notwithstanding the infrequency of sampling, combined with all the chances of such sampling being done on an unfavourable night for activity) that the 'aspect' of the garden influences the exact period (within a period of a few weeks) at which the peaks will be reached in any one garden. Likewise there is already ample evidence that the peaks vary slightly from year to year. It need hardly be stated that the peaks would also be slightly different from locality to locality.

The numbers of the various species do not fluctuate from sample to sample to the same extent. This may be taken to indicate that some species are more resistant to local weather conditions than others. For example, *Arion subfuscus* and *Agriolimax reticulatus* show distinctly fewer and less marked temporary departures from their seasonal trends than do *Arion hortensis* and *Milax gracilis*. But it is surprising to find that the last two species, which are apparently so susceptible to weather conditions, reach their peaks of activity in the winter and late autumn respectively. On the other hand, *reticulatus*, which can be considered the most resistant and hardy species, reaches its peak in what might reasonably be assumed to be the most seasonable weather for slugs. *Arion subfuscus*, which appears to be the second hardiest species, reaches its peak in the summer. This latter fact is surprising, as one would not expect any slug to reach its peak in what normally is warm dry weather.

These peaks, with the one exception of *Arion ater*, are peaks of large individuals approaching maturity and not of young ones. It will be seen later (Part 2, §§ 9 and 10) that these peaks of nocturnal activity are very closely associated with the peaks of mating (at least in those species in which mating has been observed) and with the peaks of the heaviest slugs. Detailed experimental life-history studies which include growth rates are very desirable to illuminate these and other facts brought out but unexplained by this ecological survey. But the utmost care will have to be exercised to ensure that such life-history studies are comparable with conditions in the field.

It should be emphasized that these seasonal activity curves were obtained in an attempt to discover whether there are any changes in the numbers of slugs active at the various seasons of the year. In addition to showing that there are very considerable and regular seasonal changes in the numbers of slugs active, a reasonable deduction is that these activity curves illustrate changes in population. It is extremely unlikely, for instance, that the population of *Arion hortensis* is as large in June and July as it is later in the year (see Fig. 3). It is possible, however, that there are seasonal differences in the relation of activity to population numbers. If more exact information regarding population numbers rather than the numbers active is desired, different methods must be devised. For example, marking slugs or,

what is virtually the same, introducing known numbers of a species into an area where it was previously not present should help in this direction. Equally essential is more detailed information regarding the life history of the various species.

## 7. SUMMARY

*Section 1.* The paper gives the results of an ecological study, extending over three years in certain gardens at Harpenden, Herts, of about 100,000 slugs.

*Section 2.* It is pointed out that the straw-coloured young of *Arion ater* are quite different in appearance from the more mature individuals and may easily be thought to be a distinct species.

An attempt has been made to clear up the confusion that has existed regarding the separation of the three species of *Milax*, viz. *gagates*, *gracilis* and *sowerbyi*.

The present investigations concern nine species—*Arion ater*, *A. circumscriptus*, *A. hortensis*, *A. subfuscus*, *Milax gracilis*, *M. sowerbyi*, *Agriolimax reticulatus*, *Limax maximus* and *L. flavus*. Notes are given on the characters used by the authors in distinguishing these species.

A key is appended for the separation of fifteen out of the twenty or more species which have been recorded in the British Isles.

*Section 3.* The areas used have been about 50 gardens chiefly in the Moreton End district of Harpenden. While one garden has been the main scene of the investigations, six others have been visited throughout the year and others at less frequent intervals.

*Section 4.* The method employed has been the collection of slugs seen with the aid of an electric torch chiefly on what have been thought to be favourable nights for slug activity, warm, moist, still nights being considered the ideal.

The unit sample has been the slugs able to be picked up without searching during a 30 min. walk round the area under immediate consideration.

The method and its applications are fully described.

*Section 5.* Some idea of the abundance of the slugs that are active after dark in quite ordinary suburban gardens may be gathered from the fact that 30,626 have been collected in 170 half-hour periods during 1942 and 38,416 in 181 half-hours in 1943 without the use of any baits, just by walking round the gardens with an electric torch. This gives an average for the two years of nearly 200 per half-hour. It should be remembered that the 50 or so gardens have not been chosen because they have been suspected of harbouring an unusual number of these animals. When considering the average number per half-hour one must also recall that the collecting has been done on what were judged to be favourable nights for activity and throughout the year. In the garden, roughly one-fifth of an acre in area, that has been sampled

most frequently (100 times) the average per half-hour is nearly 276; in another garden, one about half this size, that has been sampled 23 times at all times of the year the average is 296. The largest number ever picked up in any garden during half an hour has been 570 and another half-hour's collection made in the same garden over the same route after an interval of only half an hour yielded an additional 517.

Three species—*Arion hortensis*, *Agriolimax reticulatus* and *Milax gracilis*—have been found in virtually every garden, although some of them have been visited only once. The average numbers of these picked up per half-hour during the two years are respectively about 60, 50 and 40, the 1942 and 1943 totals being roughly 10,000, 11,000; 9000; and 5000, 9000. The largest numbers of these three species collected in a single half-hour are 315, 165 and 371.

Three other species—*Arion subfuscus*, *Milax sowerbyi* and *Arion ater*—have occurred sufficiently abundantly to enable 100 or more of them to be picked up in a single half-hour. The yearly totals of these species have been roughly 3000, 4000; 1000, 2000; and about 1000.

The remaining three species—*Arion circumscriptus*, *Limax maximus* and *L. flavus*—have been much less common, the totals for the two years being only 245, 222 and 10.

The section ends with a short discussion on the use of the word 'abundance' and the possibility of assessing changes in population by this collecting method of sampling active slugs.

Section 6. The total number of slugs active after

dark on nights suitable for activity has not varied greatly throughout the year and large numbers have been found at all times of the year whenever the weather conditions have been favourable.

But it is shown that each species has its own well-defined rhythm in numbers to be found active. These pulsations occur annually and in every garden with remarkable regularity whether there be large or small numbers of the species present. There have been slight variations in date according to the 'earliness' or 'lateness' of the year and the 'aspect' of the particular garden.

The species do not reach their peak numbers at the same season of the year. Most *Arion ater* have been found active in January; most *A. subfuscus* in June; *Agriolimax reticulatus* has reached its maximum numbers in June (during 1943 an 'early' year) and August–September which is probably more normal; *Milax sowerbyi* between August and October; *M. gracilis* in October chiefly, but equally large numbers have been collected even as late in the year as December; and *Arion hortensis* between October and December, closely associated with *gracilis* but, on the whole, inclined to reach its peak numbers slightly later in the year.

In the discussion various points are briefly mentioned, including the night-to-night fluctuations in numbers of the various species, the fact that the peaks of numbers active coincide with the peaks of the largest sized individuals, except in the case of *Arion ater*, and the relation between the numbers found active and the basic populations.

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*Addendum.* A species of *Agriolimax* which is intermediate in size, as well as in colour, between *reticulatus* and *laevis* may, according to Watson (1943), be conspecific with *caruanae* Poll. It re-

sembles *laevis* in its clear slime, but is generally found in gardens and cultivated places instead of in marshes.

## BRITISH ECOLOGICAL SOCIETY

EASTER MEETING 1944

## SYMPOSIUM ON 'THE ECOLOGY OF CLOSELY ALLIED SPECIES'

The Society met in the rooms of the Linnean Society, Burlington House, London, on Tuesday, 21 March 1944, the President taking the chair at 10.30 a.m. Some sixty members and guests were present. The symposium centred about Gause's contention (1934) that two species with similar ecology cannot live together in the same place, and the bearing of this, if true, on the origin and persistence of species. A distinct cleavage of opinion revealed itself on the question of the validity of Gause's concept. Of the main speakers, Mr Lack, Mr Elton and Dr Varley supported the postulate.

Mr Lack argued that, at least in birds, geographical isolation seems an essential precursor to species formation, and that if, later, two geographical races meet they may be genetically intersterile and will inevitably compete, with varying results: (i) elimination of one by the other, (ii) elimination of one at the point of overlap, but its survival over parts of its range where it is the better adapted, and so geographical replacement, (iii) habitat replacement due to adaptation to different zones of the ancestral habitat, or (iv) co-survival resulting from divergence in food preferences. It is probably only those geographical forms which have acquired some degree of ecological differentiation which are capable of persisting in the same area should they later meet. He supported his argument by reference to three groups of passerine birds, namely, Mayr's cases of passerines on remote islands, the British breeding species, and the finches of the Galapagos, and suggested that further examples were to be found among other animal groups.

Mr Elton presented an analysis of the species lists from some fifty ecological surveys of a variety of habitats. These showed a very high proportion of genera represented by single species. Figures culled from the literature on plant communities suggest similar species relationships among plants. Moreover, when two species of a genus do occur together they often prove to be different ecotypes. There is also evidence, as e.g. the grey and red squirrels in Britain, that the introduction of an extra congeneric species from outside the community may only be successful at the expense of the native species.

Dr Varley, accepting the Gaussian concept, argued that the outcome of the competition between two closely allied species depends on the differences between them and on the severity of the different

kinds of mortality. Mortality factors may be non-density dependent, e.g. the physical environment, or density dependent, i.e. competition for food and space, or destruction by predators or parasites. Together the mortality factors must destroy the surplus population. If other types of mortality are insufficient, the population density will rise until some density-dependent factor stabilizes the population density at a higher level. As mortality factors are the agents of Natural Selection, any change in the relative severity of their action will change the direction of evolution. The geographical replacement of closely allied species with similar food would be expected in continental areas, where physical factors or predators are predominant. In the absence of these factors two closely allied species will compete for the same food, and one will eliminate the other unless it will take food which the other rejects. Modified feeding habits will be favoured and will lead to adaptive radiation, as has happened among the Cichlid fishes of the African Lakes (Worthington) and the Galapagos finches where predators are absent. In plants competitive factors may lead to pure communities, as in *Mesembryanthemum* and *Brachypodium pinnatum*. Co-dominance presents a difficult problem. In chalk pastures with many co-dominants the selective advantage for rapid growth may be balanced by selection by herbivores for stunted types.

Dr Blackman presented an analysis of Harland and Martini's experiments in which eleven varieties of barley were mixed and grown under a variety of conditions, random samples of the harvested grain being sown in successive seasons up to a maximum of eleven years. The proportions of the varieties underwent marked changes, leading in various instances to suppression or dominance of one or other, or to co-dominance of two or more varieties. Arguing that varietal differences within a species may reflect interspecific differences of ecological requirements—about which critical data are lacking—it was suggested that these results indicate that competition between two species of similar ecology may or may not result in the suppression of one by the other, the final balance depending on the conditions within the habitat.

Capt. Diver made a vigorous attack on Gause's concept, on the grounds that the mathematical and experimental approaches had been dangerously oversimplified and omitted consideration of many factors

of which the importance varied among different organisms. These included sources of energy and their relative availability, predator attack, mobility, population structure and growth, individual growth rate and bulk, relation of life cycle to annual cycle, range of tolerance, means of dispersal, and the like. Pointing out the difficulty of defining 'similar ecology' he gave examples of many congeneric species of both plants and animals apparently living and feeding together. He concluded that there was little direct evidence that cohabitation or separation of related species was determined by competition for space and food, since other factors usually kept populations below the point at which serious pressure was developed.

Mr Spooner developed a similar argument, using examples from among the British wasps and bees, where populations are so restricted by the physical conditions that interspecific competition for either food or nesting sites rarely if ever becomes a limiting factor.

A lively discussion followed to which contributions were made by Mr Rose, Dr Butcher, Mr Lavender, Dr Thorpe, Miss Moore, Mr Goodall, Prof. Hale Carpenter, Prof. J. B. S. Haldane, Dr O. W. Richards, Dr Cragg, Dr Jones, Dr Uvarov,

and Dr Clapham. The arguments pro and contra were fairly evenly balanced. Instances of mutually exclusive congeneric species included the *distans* section of *Carex*, the *pimpinelloides* section of *Oenanthe*, species of *Limonium*; while genera with species living together included *Drosera*, *Betula*, *Orchis*, *Ranunculus*, *Cimex*, *Drosophila*, *Pseudarcaea* (in Uganda), downland grasses, *Limnaea*, *Asellus* and others. Points made included: that in running water competition is characteristically between organism and physical environment rather than interspecific (Dr Butcher); that habitat preferences are often genetically fixed and may result in, and not from, geographical isolation (Dr Thorpe); while Prof. Haldane referred to the unseen competition of one species acting as a carrier of a parasite fatal to another, and to the need for research on the history of diseases of closely related species.

Those interested in the subject of the symposium may care to refer to two papers relating to it, which have been prepared by speakers who took part in the discussion. Mr Lack's paper has been published in the July number of *Ibis*, while Mr Elton's will be published in a forthcoming number of the *Journal of Animal Ecology*.

## REVIEWS

## THE JOURNAL OF ECOLOGY

(Vol. 32, No. 1, May, 1944)

This number contains a long Report by the British Ecological Society on Nature Conservation and Nature Reserves. It deals mainly with the methods recommended to be employed in Nature Conservation and with the machinery which will be required to implement the recommendations. A central Wild Life Service is envisaged. The number also contains various contributions on the ecological principles involved in the practice of forestry, these being reports of a symposium held by the British Ecological Society in July, 1943. They cover a very wide range of interests.

An original paper by C. B. Williams deals with some applications of the logarithmic series and the index of diversity to ecological problems. Apart from the discussion of mathematical theory a large number of examples is discussed, including the following: the numbers of species in typical plant communities; the distribution of numbers in samples of lice, of trapped mosquitoes and of species in collections of butterflies; the grouping of species in genera and of genera within families.

A further contribution to the Biological Flora is included, dealing with *Tamus communis*, by I. H. Burkill.

The number concludes with the annual reports of the British Ecological Society.

W. H. PEARSELL

**L. R. Dice (1943).** *The biotic provinces of North America*. 78 pp. Map. University of Michigan Press, Ann Arbor. Price \$1.75.

Dice's *Biotic Provinces of North America* is the most recent biogeographic effort to erect a framework into which to fit the numerous plant and animal communities of the North American continent. The conception is both original and daring, combining the viewpoint of the physical geographer with that of the biologist. Dice's wide field experience has given him a first-hand knowledge of a considerable part of the continent, although the space is so vast and conditions so varied that no one man can know every community. The work is essentially that of the field man, rather than that of the laboratory or library investigator. This is not to say that the library has been neglected, as the 152 titles in the list of literature cited show.

The well-known division into life zones based on temperature, but distinguished on the ground by vegetation, devised by C. Hart Merriam and widely used by the U.S. Biological Survey (now part of the Fish and Wildlife Service) and other naturalists, is not followed, except that the zones resulting from differences in altitude on mountains are recognized as 'life belts'. Although Dice is an animal ecologist, his biotic provinces are based largely on vegetation, though differences in the fauna are used as well as climate, physiography, and soil. This is reasonable in that plants are fixed, and so have been more studied and are better known than animals. Also, vegetation directly and indirectly con-

trols the distribution of animals through food, shelter, nesting sites, etc.; and, furthermore, the natural vegetation is an indicator of the sum total of the environmental factors. It is perhaps not without significance that in the United States, a country in which natural conditions still exist here and there, plant ecologists and animal ecologists try to work together from the viewpoint of the community as a unified whole, made up of plants, animals, and inanimate physical forces.

Dice's biotic province 'covers a considerable and continuous geographic area and is characterized by the occurrence of one or more important ecologic associations that differ, at least in proportional area covered, from the associations of adjacent provinces. In general, biotic provinces are characterized also by peculiarities of vegetation type, ecological climax, flora, fauna, climate, physiography, and soil'. The definition may be criticized as being too subjective, and as giving the author too wide scope in laying out his provinces. Thus one might say that 'a considerable area' sounds rather vague, or that the importance of an association might be a matter of individual judgment, or again that differing 'in proportional area covered' gives an opportunity for splitting hairs if desired. Yet these provisions in the definition are not without justification. That for a considerable area is obviously designed to rule out small units which would result in recognizing too many provinces, and would thereby make the system so cumbersome as to be unusable. The importance of an association is based on the opinion of a considerable number of ecologists, and is a matter on which agreement is pretty general, at least for associations large enough to be considered in delineating biotic provinces. The 'proportional area' proviso covers instances in which an association may be widespread in one area and play a minor part in another. It will be noticed that each biotic province is 'continuous', and therefore takes in a solid block of country, unlike Merriam's life zones which are discontinuous.

Three subdivisions are provided for: the biotic district, the life belt, and the ecologic association. The biotic district covers a definite and continuous part of a biotic province and is distinguished by ecological differences of less importance than those which separate biotic provinces.

A life belt is a vertical subdivision of a biotic province. An example is the vertical zonation on mountains due to altitude, in which, for example, the lowest belt may be open-grown piñon pine and juniper, above which occurs western yellow pine, and above that Douglas fir, and so on. Life belts would be discontinuous, as a biotic province takes more than a single range of mountains. Dice thinks of each life belt as limited to a single province because each province is distinct in its environmental factors and flora and fauna, though similar life belts occupy corresponding positions in adjacent provinces. This might be denied at first sight, because one could point, for example, to forests of pure western yellow pine on the west slope of the Sierra Nevada Mountains in California, in eastern Oregon, in Arizona and New Mexico, in Colorado, and in the Black Hills and South Dakota, that is, in five biotic provinces, and hundreds

of miles apart. Yet, although superficially similar, the yellow pine forests in each of these provinces are growing under conditions different enough to necessitate different silvicultural methods in each. I believe that there are also considerable differences in the fauna. The author has made very little use of his subdivision into biotic districts in his description of the individual biotic provinces. In some of the descriptions he mentions districts and life belts described by other authors, but in none of them has he attempted to try to delineate a district.

An ecologic association is defined as 'any ecologically uniform and relatively stable community below the rank of life belt and biotic district. The name is applied to well-marked successional stages as well as to the climatic or edaphic climax of an area'. One might think that a life belt, by its very nature, would generally contain only a single association, but some of the life belts, as the western yellow pine and the lodge-pole pine, are interrupted here and there on level places by grassy openings known as 'parks', which are of an apparently rather stable nature and would correspond with the foregoing definition of an association.

Dice specifically disclaims finality for his biotic provinces. The ecological information is insufficient to make this possible. His map avoids the common fault of creating confusion through including too much, but goes to the opposite extreme. There is so little on it besides the outlines of the biotic provinces that, unless the reader has a very good knowledge of the country, he will need a set of more detailed maps to follow the boundaries as given in the descriptions. This is rather a drawback for those outside of North America who are interested in the biogeography of that continent.

The provinces vary greatly in size, as would be expected. The largest is the Hudsonian, covering about three-quarters of the area of Canada below the Arctic regions which Dice calls the Eskimoan province. There are 28 provinces in all, of which 4 are in Canada and Alaska, 4 in Mexico and 20 in the United States, excluding Alaska. Of these 20, five extend north into Canada, and five others reach down into Mexico. Some of the provinces include striking contrasts. For example, the Californian includes the semi-arid central valley and the heavily forested Sierra Nevada mountains culminating in Mt Whitney, the highest peak in the United States outside of Alaska. Such contrasts are, of course, inevitable in mountainous country, such as that west of the Great Plains, and could be avoided only by splitting the map into innumerable spots for each mountain range and valley. As a matter of fact, it is rather surprising to find that each of these large provinces, with all its contrasts and diversity, is characterized by its own peculiar set of conditions which make it distinctly different from adjacent provinces. On the whole, judging by the parts I have seen of 14 provinces out of the 20 wholly or partly in the United States, the division has been well made, and there is a strong ecological basis for each province. The exact location of some of the boundaries must be a matter of individual judgment because of the gradual change in conditions from one place to another. This applies particularly in level country, while in mountains there is the difficulty of deciding in which province to place an area that is not characteristic of either of two adjacent provinces. South central Oregon is an example, and has been included in the Californian province

though it could have been included in the Oregonian (p. 32).

There is a brief description of each province. The whole 28 are covered in only 55 pages of large type, and of this limited space a proportion that seems unnecessarily large is devoted to the reason for the name. For each province the description includes, besides the names used by earlier writers, the characteristic vegetation, precipitation, temperature, and brief mention of some of the animals, especially those restricted to the province. The descriptions, with but few exceptions, seem to be accurate and give a great deal of information in a very small compass. One of the few exceptions occurs in the description of the climate of the Californian province (p. 47), in which the author says 'The climate of the Californian province is notable in that, *except in the mountains*, almost no precipitation falls during the summer months' (italics are reviewer's). The mountains should not have been excepted, because they also receive very little precipitation in summer. It is true, as he says, that on the western slopes of the Sierra Nevada mountains thunderstorms are frequent in summer. But these thunderstorms are accompanied by very little rain. They are really lightning storms which cause frequent forest fires, as I well know from a summer spent in those mountains during which fighting forest fires was not an uncommon experience. At the same time the lack of rain makes the Sierra forests extremely pleasant to camp in: always fine weather, no mosquitoes, and yet well watered from the abundant snows of winter, which amount to 300-400 in. (25-33 ft.).

With such brief descriptions it would be extraordinary if there were no omissions. One of the most noticeable is in the description of the Montanian province which includes the northern Rocky Mountains. The very important forests of western white pine (*Pinus monticola*), principally in Idaho, are not mentioned.

The book is well printed and free from typographical errors. The only one noticed is in the description of the Mohavian province on p. 54 in which south-eastern Utah should obviously be south-western Utah. The index is not altogether satisfactory. One could not well ask for completeness, because, in a work of this kind a complete index would have to be almost as long as the book itself. But one wonders why the Douglas fir, which is such an important tree in several biotic provinces, is not included while many less important ones are.

It is not to be anticipated that Dice's system of biotic provinces will be accepted by everyone. Many animal ecologists will probably prefer Merriam's life zones, and plant ecologists will prefer Clements' communities. The test will be its workability, and I believe that it will be found workable and a useful framework. Undoubtedly it will be modified as more information accumulates and as it becomes possible to fill in the details.

It would be a fine thing if samples of the characteristic community in each biotic province could be set aside and preserved in their original condition for future study. Such samples are already being preserved in seven provinces in National Parks and National Monuments (a class of reservation below, but often leading to, a National Park) though unfortunately some of the waters in most of the National Parks have been stocked to improve the fishing and so are no longer entirely natural.

BARRINGTON MOORE

## NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) by non-subscribers, from the Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, G. Elton, R. B. Freeman, B. M. Hobby, Barrington Moore, F. T. K. Pentelow and H. N. Southern.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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### 1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

#### (a) MARINE AND BRACKISH

**Went, A. E. J. (1944).** 'Brief histories of Irish fisheries. II. The Galway fishery—methods of fishing.' *Salm. Trout Mag. Lond.* No. 110: 27-39.

An historical account of the methods of catching salmon in the Galway River. They include fishing weirs, nets, spears and angling.

**Went, A. E. J. (1944).** 'The Galway fishery. An account of the modes of fishing together with notes on other matters connected with the fishery.' *Proc. R. Irish Acad.* 49 C, no. 5: 187-219.

An historical account from A.D. 1508.

**Jepps, M. W. (1942).** 'Studies on *Polystomella* Lamarck (Foraminifera).' *J. Mar. Biol. Ass. U.K.* 25: 607-66.

Cultivation of *Polystomella crista* in diatom cultures (*Navicula mutica* var.) is described. Schizogony and sporulation are discussed and it is concluded that a complete life cycle—of one microspheric and one megalo-spheric phase—takes about two years.

- Lowndes, A. G. (1943).** 'Some applications of the displacement method of weighing living aquatic organisms.' *Proc. Zool. Soc. Lond. A*, 113: 28-43.

A considerable amount of new data is given on density, sinking factor, water and fat content of a number of marine organisms and tissues. In the Decapods density of ripe eggs and embryos is high while they are being carried by the parent, but decreases before the larva starts a free-swimming existence. In echinoderms density is low at an early stage, so that the embryos progress satisfactorily with cilia.

(b) FRESH WATER

- Went, A. E. J. (1944).** 'A note on the habits of the common lizard, *Lacerta vivipara* Jacq.' *Irish Nat. J.* 8: 181.

Lizard swimming in a small lough in Galway.

- Brown, R. H. (1944).** 'Notes on a pair of moorhens.' *Brit. Birds*, 37: 202-4.

Details are given on nest-building, incubation and nesting success.

- Newton, L. (1944).** 'Pollution of the rivers of West Wales by lead and zinc mine effluent.' *Ann. Appl. Biol.* 31: 1-11.

Summary, with references, of investigations done on Cardiganshire streams during the past 20 years. Galena and zincblende on old dumps and slime pits are oxidized by weathering into their sulphates which surface water dissolves and carries into rivers. The presence of zinc is as serious a pollution as that of lead, more deleterious in the case of plants. The dump areas are not colonized by plants, partly because the coarse material weathers very slowly, partly on account of blown material from old slime pits and probably also owing to phosphate deficiency. Detritus from the mines covering the river beds mechanically deters the establishment of macrophytes and reduces the microflora with the result that caddis-fly larvae are absent. There is a sequence for the disappearance of the fauna of a polluted stream; on recovery the reverse sequence may be expected to be followed. The same phase is visible in passing downstream from the source of pollution. The formation of an adsorption complex of the heavy metals on the gills of fish, together with an excess secretion of mucus, causing suffocation is the cause of their death.

- Sawyer, R. E. (1944).** 'Nature of the acid in soft water in relation to the growth of brown trout.' *Nature, Lond.* 153: 55-6.

The acidity of certain Highland waters was found to be due solely to the presence of CO<sub>2</sub> and not to any organic acid. It is suggested that CO<sub>2</sub> is not an inhibiting factor, but that some deficiency might affect the growth of the trout.

- Pentelow, F. T. K. (1944).** 'Nature of acid in soft water in relation to the growth of brown trout.' *Nature, Lond.* 153: 464.

The acidity of Highland waters was found to be due mainly to CO<sub>2</sub> after a dry period, but also to organic acids after heavy rain. The poor growth of trout may be due to the very low egg and juvenile mortality with consequent high populations relative to the available food.

- Marshall, J. F. (1944).** 'The morphology and biology of *Culex molestus*: observational notes for investigators.' British Mosquito Control Institute, Hayling Island, Hampshire. Price 1s. (Director's war-time address: 'Wayside', 47 London Road, Cheltenham.)

Differences in structure, life history and habits of *Culex pipiens* and *molestus* are fully compared. *Molestus* is one of the few mosquitoes that can mate in a small cage and produce fertile eggs without a blood-meal, though the fertility is three times higher with a blood-meal, and it is a fierce man-biter. It can breed all the year round, and can be reared in the laboratory. It apparently breeds only or mainly in underground or dark stagnant water. It does not breed in open (e.g. static water) tanks. Its distribution so far known is in or near London, in Harwich and in Hull, and it may be introduced possibly from the Continent. It may be spreading in London through the Underground railways. Notes are given on the application of known control measures to *Culex molestus*, and on the methods of rearing and breeding it. Good bibliography.

- Classey, E. W. (1944).** '*Culex apicalis* Adams (Dip., Culicidae) in Great Britain.' *Entomologist*, 77: 98-9.

A single fourth instar larva of *Culex apicalis* was found by J. Staley at Ascot on 31 July 1936. This was the sixth record of this species in Great Britain, and the third recorded larva.

- Walton, G. A. (1944).** 'An authentic record of *Micronecta minutissima* L. (Hemipt., Corixidae) in Britain.' *J. Soc. Brit. Ent.* 2 (5): 165-6.

On 3 June 1943, in Longleat Park, North Wiltshire, large numbers of *Micronecta* were seen in the shallows of Petit Jean's Island Pond. A count revealed 146 *M. minutissima* and 287 *M. scholtzi* in a random sample. The previous evidence for the inclusion of *M. minutissima* in the British List was five old specimens from the Harwood and Fowler collections and a single female from the Hebrides. No other *Micronecta* were captured in this or other pools in Longleat Park during the previous four years!

- Collenette, C. L. (1944).** 'Odonata avoiding limestone country.' *Entomologist*, 77: 61.

The mountain limestone formation in Derbyshire, which lies between Buxton, Castleton, Bakewell, Matlock and Thorpe, an area of roughly 9 miles by 15, appears to be singularly deficient in dragonflies. Towards the south of this limestone area, but well inside it, to the west of Minninglow Hill, in a district of bare grassy slopes and stone walls at 1000 ft., is a disused sandpit, containing a pond of clear deep water with some fine trout. This supports *Coenagrion puella*, *Pyrhosoma nymphula*, *Ischnura elegans* and *Enallagma cyathigerum*, which do not occur in waters on the surrounding limestone.

- Hickin, N. E. (1944).** 'Chartley Moss and the caddis fly *Neuronia clathrata* Kol. (Phryganeidae, Trichoptera).' *Entomologist*, 77: 20-21.

This caddis-fly is confined to very few localities, but is abundant at Chartley Moss, Staffordshire. The area involved is but a few acres among farm land.

- Sawyer, F. E. (1944).** 'Swimming nymphs and their imitation: recent observations of the process of hatching.' *Salm. Trout Mag. Lond.* No. 111: 149-54.

An account of the transformation, under natural conditions, from the nymph to the sub-imago in certain species of Ephemeroptera. They are identified only by their popular names, but appear to include *Baëtis vernus*, *B. bioculatus* and *B. pumilus* and *Ephemerella ignita*.

- Lloyd, B. (1944).** 'West Hertfordshire dragonflies.' *Trans. Herts. Nat. Hist. Soc. Fld Cl.* 22: 43-7.

Records of 13 species with some ecological notes particularly on oviposition.

- Attlee, H. G. (1943).** 'A key to the identification of east Sussex dragon-flies.' *Hastings Nat.* 6: 115-24.

Key to 31 species based largely on the more obvious external characters. A few notes on flight characteristics of adults, and dates of earliest and latest Sussex records, are given.

- Killington, F. J. (1944).** 'A new locality for *Ischnura pumilio* (Charp.) (Odon., Coenagriidae).' *Ent. Mon. Mag.* 80: 12-13.

This dragonfly has hitherto been known with certainty to exist in only one restricted locality in the New Forest. It is now reported from Alderney Heath on the northern outskirts of Parkstone, Dorset and in a *Sphagnum* bog bordering the River Bourne.

- Longfield, C. (1944).** 'A further new locality for *Ischnura pumilio* (Charp.) (Odon., Coenagriidae).' *Ent. Mon. Mag.* 80: 70.

This rare dragonfly was discovered in the Isle of Purbeck in 1943.

- Scourfield, D. J. (1943).** 'The post-embryonal development of the male of *Daphnia magna*.' *J. Quekett Micr. Cl.* 1: 276-83.

Description with plates of the head, valves, antennules etc. in the various stages. Includes a note on food for *Daphnia* cultures: droppings of horse and rabbit mixed in water with green algae and soil.

- Scourfield, D. J. (1943).** 'The Entomostraca of the bottom deposits of Windermere.' *Proc. Linn. Soc. Lond.* 154: 253-8.

Twenty-three species of Cladocera and a single specimen of an Ostracod were found in cores from various depths. These species occur in the oldest deposits and, with the exception of *Bosmina longispina*, are the same as those in the lake to-day.

- Kennard, A. S. (1943).** 'The Post-Pliocene non-marine Mollusca of Hertfordshire.' *Trans. Herts. Nat. Hist. Soc. Fld Cl.* 22: 1-18.

Gives lists, with estimates of abundance, from three Pleistocene and ten Holocene deposits. Some comparisons with present distribution and climatic conditions are made.

(c) LAND

**Lloyd, L. C. (1944).** 'Effects on bird-life of the severe winter of 1939-40.' Trans. Caradoc Fld Cl. for 1941, 11: 207-15.

Numerous records of the effect of prolonged cold, both decreasing small, mostly resident species and increasing winter migrants, particularly geese and duck.

**Cox, P. R. (1944),** 'A statistical investigation into bird-song.' Brit. Birds, 38: 3-9.

Data are given on the number of times certain species were heard singing from two frequently traversed standard routes. Comparison is made between frequency of morning and evening song. The former is greater in volume (i.e. number of individuals  $\times$  frequency of singing) than the latter, except in the case of the blackbird. The fact that the counts were taken at the same time of day regardless of sunrise and sunset makes these results dubious except in a very broad way.

**Ryves, B. H. (1944).** 'Nest-construction by birds.' Brit. Birds, 37: 182-8, 207-9.

The parts played by the sexes in nest construction are defined from first-hand observation of certain species. There is considerable variation from species to species.

**Ryves, B. H. (1944).** 'The fledging period of birds.' Brit. Birds, 37: 151-4.

It is suggested that to avoid ambiguity the fledging period should be taken as the time 'during which the young remain in the nest, which they finally abandon under natural conditions in varying stages of general development'.

**Pullen, N. D. (1944).** 'Drumming of the great spotted woodpecker.' Brit. Birds, 37: 175-6.

By fixing a microphone to the trunk of a tree used for drumming it is shown that the beak definitely makes contact with the wood. It is suggested that the carrying quality of the drumming and the fact that few beak marks are found may be accounted for by the bird picking out places that will resonate at a certain frequency of blows.

**Davidson, J. (1944).** 'On the relationship between temperature and rate of development of insects at constant temperatures.' J. Anim. Ecol. 13: 26-38.

A general empirical curve to show the relationship between temperature and time required for development in insects is based on the formula:

$$\frac{1}{y} = \frac{K}{1 + e} a - bx,$$

where  $1/y$  is the reciprocal value of the time for a given stage in the life cycle of an insect to develop at a given temperature  $x$ ;  $K$ ,  $a$  and  $b$  are constants. Data on five insects obtained by other workers were fitted to this curve, which faithfully represents the speed of development for 85-90% of the range at which development can go on.

**Edelsten, H. M., Fryer, J. C. F. & Robinson, A. (1944).** '*Hydrillula palustris* Huebner in England.' Entomologist, 77: 49-54, 65-72.

One of the few species of British moths of which the life history and habits are still relatively unknown. Its distribution, variation, habits, egg, larva, larval habits and pupa are discussed. The Ichneumon parasite *Campoplex terebrator* was bred. The species is found in fens, not the more luxuriant parts where the vegetation is dense and high, but rather where there is a tussocky growth of grass, e.g. of *Calamagrostis epigeios* with patches of *Spiraea*. This combination is generally found in the drier parts of a fen, e.g. at the sides of droves, and also where the vegetation has been checked periodically by cutting.

**Russell, A. G. B. & de Worms, C. G. M. (1944).** 'A new locality for *Amathes alpicola* Zett. (Lep. Agrotidae).' Entomologist, 77: 1-4.

This elusive moth occurs on mountain tops in the Scottish Highlands. Numerous pupae and even larvae on the point of metamorphosis were taken from beneath moss adjacent to crowberry (*Empetrum nigrum*) at the end of May 1942, near Aviemore, about 2000 ft.

**Russell, A. G. B. (1944).** 'Moths taken in the neighbourhood of Gatehouse-of-Fleet, Co. Kirkcudbright.' Entomologist, 77: 90-2.

There are few previous records from south-west Scotland.

**Grensted, L. W. (1944).** 'A mid-winter appearance of *Macroglossum stellatarum* L. (Lep., Sphingidae).' Ent. Mon. Mag. 80: 42.

This moth was seen in full activity at Oxford on 13 January. The species is capable of true hibernation, but only for a short period, and is probably never successful in living through an English winter, though specimens have often been recorded even as late as March.

**Hobby, B. M. (1944),** '*Macroglossum stellatarum* L. (Lep., Sphingidae) in flight in April.' Ent. Mon. Mag. 80: 87.

Observed in Warwickshire 10 April 1944.

**Thompson, G. H. (1944).** '*Coccinella quadripunctata* Pont. (Col., Coccinellidae) in Berkshire.' Ent. Mon. Mag. 80: 42.

This ladybird, added to the British list in 1943, has now been found under bark of larch at Tubney, Berks.

**Jacob, F. H. (1944).** 'Notes on the habits and life history of the leaf-eating brown weevil, *Phyllobius pyri* L. (Col., Curculionidae).' Ent. Mon. Mag. 80: 78.

Records of damage to wheat (probably accidental) and to fields of hill grazing, mainly bents and fescues (probably one of the less important factors in the deterioration of this type of pasture).

**Cohen, M. (1941).** 'The biology of the poplar leaf-mining beetle, *Zeugophaga subspinos* F. (Chrysomelidae).' Yearb. N.W. Nat. Union, 1941: 25-33.

This is one of three British species, and has a southern and midland distribution. It feeds on poplars, and in the present study was found on *Populus nigra* and *P. alba*. Its life history and habits are described, with line drawings of the stages, and some photos. High density built up in dense poplar plantations, and injury was caused, especially at 6-12 ft. from the ground. The adults emerge from the soil in July and attack the undersides of the leaves. The eggs are laid from below, but the larval mine develops in the upper layer of the leaf. The fourth instar larvae leave the leaves for the ground in late summer or autumn, and pupate next spring and summer. Other insects mentioned as attacking poplar leaves are the moth caterpillar *Acronycta megacephala* in early summer; the sawfly *Trichiocampus viminalis* later in summer; and the beetle *Phyllodecta vitellinae* in July. The combined effect of these four species can cause semi-defoliation. Braconid larvae were occasionally found as ectoparasites of the larvae of *Z. subspinos*.

**Wright, D. W., Petherbridge, F. R. & Ashby, D. G. (1944).** 'The biology and control of the carrot fly.' J. Minist. Agric. 51: 11-15.

The first generation continues to emerge at Chatteris (Isle of Ely) from fen soil until well into August, whereas on the medium loam of Cambridge it ends abruptly about mid-June.

**Fraser, F. C. (1944).** '*Kimminsia rava* (Withycombe) (Neur.) at Bournemouth.' J. Soc. Brit. Ent. 2 (5): 182-3.

Newly emerged specimens of this rare lacewing seen in very large numbers on tree trunks. The adult life appears to be spent in the tree-tops, which would account for its apparent rarity.

#### (d) SMALL ISLANDS

**Rutledge, R. F. (1944).** 'Results of exploration in search of Leach's fork-tailed petrel, *Oceandroma l. leucorrhoea* (Vieill.).' Irish Nat. J. 8: 180.

Islands off Donegal, Galway and Kerry all negative in 1943.

## 2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

**British Ecological Society Committee (1944).** 'Nature conservation and nature reserves.' J. Ecol. 32: 45-82; J. Anim. Ecol. 13: 1-25.

The B.E.S. Committee agrees with some of the conclusions in the report by the quasi-official Nature Reserves Investigation Committee on 'Nature Conservation in Great Britain', March, 1943. It supports the N.R.I. Committee's two conclusions: (1) to separate National Reserves from Local Reserves, and (2) to form local committees to obtain adequate information on areas to preserve. The B.E.S. Report gives a wider and interesting survey of the position of vegetation and wild life, and their prospects of survival, and suggests several

new lines for policy. The three objectives of nature reserves are: (1) preservation of characteristic British scenery for the enjoyment of the people, (2) education, and (3) scientific research. Many reserves can be made to serve all three purposes. Other land uses, especially agriculture and forestry, must be considered; and adjustment should be sought with shooting and hunting interests concerning predators. Expert management, based on ecological knowledge and practical experience, is essential in all National Parks and in nearly all National and Local Reserves. With semi-natural vegetation, as much of it is, the activities which produced it (grazing, burning, etc.) must be continued to prevent changes and the disappearance of the desired plant communities with their characteristic animals. Most communities of invertebrates will be automatically protected by the preservation of the vegetation. For the conservation of fish and other aquatic animals and plants the most important measure is the prevention of pollution. Only a few species of Amphibia and reptiles are local and need protection. Birds and mammals, owing to power of movement, cannot be conserved solely by setting aside land areas; the proper density and distribution of the species must be maintained by active management based on knowledge gained by research applied to the field problem. Rare species will require 'sanctuaries' or 'species Reserves' to protect the breeding stock. Introduction of exotic species should be prohibited except under special license. Scheduled areas, in which further development would be prohibited or restricted, would protect communities of flora and fauna of scientific interest. An educational campaign is recommended, by illustrated regional booklets, use of nature reserves as centres of education in field natural history, handbooks for each reserve, and lectures and field trips. The conclusion of the N.R.I. Committee that 'The Government should take formal responsibility for the conservation of native wild life both plant and animal', is strongly supported. The B.E.S. Committee urges that a National Wild Life Service be established as the central authority embracing the whole field of conservation of the native flora and fauna.

**Williams, C. B. (1941).** 'Some applications of the logarithmic series and the index of diversity to ecological problems.' *J. Ecol.* 32: 1-44.

The logarithmic series developed by Fisher (*J. Anim. Ecol.* 12: 42-8, 1943), when applied to a number of problems of the division of individuals and of species into genera, in both animals and plants, fits extremely well. If it is convergent, both the number of units (e.g. individuals) and of groups (e.g. species) can be summed. When several samples are taken from a population containing a number of species the ratio  $n_1/x$  (where  $n_1$  is the number of groups with 1 unit, and  $x$  is a constant less than unity) is constant and characteristic of a population, and has been called the index of diversity.

**Kirk, J. C. & Wagstaff, R. (1943).** 'A contribution to the study of the Scottish wild cat (*Felis silvestris grampia* Miller).' *Northw. Nat.* 18: 271-5.

Gives a standard method of taking measurements and full details for 107 specimens of which only five were females, taken in Scotland between 1919 and 1939.

**Corbet, A. S. (1943).** 'Taxonomy of the moths infesting stored food products.' *Nature*, Lond. 152: 742-3.

It is only in the past forty years that the male external genitalia have been used to distinguish different species of moths. The old criteria of wing- and body-colour patterns are insufficient to separate certain species-complexes, the members of which may also have very similar ecology in the adult phase. However, there may be quite different food habits among the larvae.

**Corbet, A. S. & Tams, W. H. T. (1943).** 'Key for the identification of the Lepidoptera infesting stored food products.' *Proc. Zool. Soc. Lond. B*, 113: 55-148.

**Cameron, M. (1944).** 'On the British species of the genus *Tachyporus* Gr. (Col., Staphylinidae).' *Ent. Mon. Mag.* 80: 16-17.

Key to the species of these common flower-frequenting beetles.

**Kimmins, D. E. (n.d., 1943 or 1944).** 'Key to the British species of aquatic Megaloptera and Neuroptera.' *Sci. Publ. Freshw. Biol. Ass. Brit. Emp.* No. 8: 1-20.

A further very useful addition to this series, dealing with the life histories, habitats, and identification of the two species of alder-flies (*Sialis lutaria* and *fuliginosa*) and the four species of lacewings (*Osmylus fulvicephalus* and *Sisyra terminalis*, *fusca* and *dalii*) that form the aquatic representatives of these two orders in Britain. There is a short bibliography.

**Lebour, M. V. (1942).** 'The larvae of the genus *Porcellana* (Crustacea Decapoda) and related forms.' *J. Mar. Biol. Ass. U.K.* 25: 721-37.

A detailed study of *P. longicornis* and *P. platycheles* larvae in inshore waters. It was thought that a third species was present at Plymouth, but this was proved to belong to *P. platycheles*.

## 3. PARASITES

**Taylor, E. L. (1944).** 'A search for endemic areas of trichinosis in Great Britain.' *Nature*, Lond. 153: 745-6.

Outbreaks of trichinosis in 1940-1 at Wolverhampton, Penrith and Harpenden were not attributable to imported meat. Since the incidence of *Trichinella spiralis* is very low in rats, a quicker method of detecting unknown endemic areas was attempted by examining the rat's predators—whose skeletal muscles would show whether or not they had ever eaten infected animals. No larval parasites were found in 716 stoats, weasels and polecats sent in by pests officers from 39 counties.

**Birkett, N. L. (1944).** 'The natural control of *Pieris brassicae* by its Braconid parasite—*Apanteles glomeratus*.' *Entomologist*, 77: 13-14.

A count in a pupation site gave 473 clumps of parasite cocoons, and 21 normal pupae of the cabbage white butterfly, i.e. an infestation of 96%.

**Beirne, B. P. (1943).** '*Argyresthia conjugella* Zell., and other Lepidopterous pests in Ireland during 1942.' *Econ. Proc. R. Dublin Soc.* 3: 163-71.

No parasites of *A. conjugella* were reared from Irish larvae, but most of the seven known parasites of this moth have been captured in Ireland.

**Blair, K. G. (1944).** 'Further notes on the galls of *Lipara lucens* Mg. (Dipt., Chloropidae).' *Ent. Mon. Mag.* 80: 6-7.

*Lipara lucens* forms large cigar-like galls found on the common reed *Arundo phragmites*. Notes on the parasites *Polemon liparae* (Braconidae) and *Stenomalus liparae* (Chalcid) are given. Also on the inquiline *Haplegis* (Chloropidae) and *Perrisia inclusa* (Cecidomyiidae).

**Walker, M. J. (1943).** 'Notes on the biology of *Dexia rustica* F., a dipterous parasite of *Melolontha melolontha* L.' *Proc. Zool. Soc. Lond. A*, 113: 126-76.

In Britain this species is the only recorded parasite of the chafers, whose larvae ('white grubs') cause serious damage to plants and young trees. An investigation of the biology of this parasite shows it to be confined to the region south of the Wash; the rate of parasitism in the host population is generally small, though that of individuals may be high. The age distribution of the host larvae, which take four years to mature, varies according to whether generations overlap or not; where they do this only to a small extent or not at all, the parasite, which matures in a year, must have considerable difficulty in surviving.

**Melville, R. & Dade, H. A. (1944).** 'Chalk brood attacking a wild bee.' *Nature*, Lond. 153: 112.

A wild bee's tunnel in a piece of wood was found to contain a pollen store gathered from a single species of plant (a habit regarded as characteristic of the honey bee). The pollen was covered with the fungus which produces chalk brood in honey bees.

## 4. FOOD AND FOOD HABITS

**Rudra, M. N. (1944).** 'Manganese hunger in animals.' *Nature*, Lond. 153: 111-12.

Rabbits deprived of manganese eagerly ate wood, cork and each other's fur. Rats showed similar symptoms and eventually died.

**Hodgson, S. B. (1944).** 'Lepidoptera eaten by bats.' *Entomologist*, 77: 62-3.

A bats' roost in a shed on the edge of Brampton Wood, Huntingdonshire, provided evidence of the following prey: Rhopalocera, 1; Bombyces, 11; Noctuae, 45; Geometrae, 13; Hepialidae, 1; and numerous remains of *Tortrix viridana*—72 species in all.

**Donisthorpe, H. (1944).** 'Mice eating insects, etc.' *Ent. Rec.* 56: 22.

Circumstantial evidence of a house-mouse eating house cricket and spider. Also of mice destroying a collection of beetles.

**Malcolm, M. C. (1944).** 'Mice eating moths.' *Ent. Rec.* 56: 59.

Mice eat the bodies of the moths *Ephestia sericarium* used for experimental purposes. It was impossible to say whether the mice eat live moths or only dead ones. References to other published records are given.

**Williamson, H. (1944).** 'They take 10,000 mice in a year.' *Bird Notes & News*, 21: 23-4.

The statement is made that one pair of barn owls watched through one night brought over 100 'mice' to the nest; in the morning 43 'mice, voles and young rats' were counted round the nest, and by 3 p.m. they had all been eaten.

**Pirenne, M. N. & Crombie, A. C. (1944).** 'White plumage of sea-birds.' *Nature*, Lond. 153: 526-7.

When the sky is overcast black birds may be seen from farther away than white birds; but in sunshine they may be more conspicuous. However, the stimuli which make fish dive are not known.

**Craik, K. J. W. (1944).** ['White plumage of sea-birds.'] *Nature*, Lond. 153: 527.

There is probably some advantage in white plumage if a fish dives as soon as the bird reaches threshold visibility.

**Armstrong, E. A. (1944).** ['White plumage of sea-birds.'] *Nature*, Lond. 153: 527-8.

The suggestion that white coloration is adaptive is questioned because (1) many white birds are scavengers, or feed on animals with weak sight, (2) kingfishers, cormorants, etc. are not white, (3) immature birds are not known to be handicapped by the absence of adult white plumage, (4) white may be related to relative immunity from predators because of the bird's size.

**Ingram, G. C. S. (1944).** 'Feeding habits of the black-headed gull.' *Brit. Birds*, 38: 12-13.

**Boyd, A. W. (1944).** 'Attacks on diving birds by black-headed gulls.' *Brit. Birds*, 38: 14-15.

First-hand observations showed that black-headed gulls frequently attack water birds. The first author states that he has never been able to confirm that this is to secure food: the second author gives a number of instances showing that such predation does in fact occur.

**Adolph, P. A. (1944).** 'Some food remains left in a black redstart's nest after the young had fledged.' *Brit. Birds*, 38: 16-17.

A miscellaneous collection of arthropods among which Diptera predominated. The nest was from the Temple, London.

**Ware, A. Hibbert- & Rutledge, R. F. (1944).** 'A study of the inland food habits of the common curlew.' *Brit. Birds*, 38: 22-7.

Faecal pellets and evacuated gizzard linings collected from a roosting place gave information, mostly qualitative, on food habits from July to February. There was great diversity, but Coleoptera seemed to predominate. The gizzard linings were not only evacuated through the bill, but also passed through the intestine, leaving characteristic brown gelatinous faeces.

**Ellison, N. F. (1943).** 'Food-pellets cast up by the blackbird.' *Northw. Nat.* 18: 313-14.

Record of blackbird producing pellets formed from 'seeds' in a matrix of fleshy skins of *Laburnum*, hawthorn and loganberry.

**Allan, P. B. M. (1944).** 'Foodplants of *Vanessa cardui* L.' *Ent. Rec.* 56: 60.

*Carduus arvensis*, *C. lanceolatus*, *C. nutans*, *C. crispus*, *Onopordon acanthium*, *Arctium minus*, *Echium vulgare*, *Malva sylvestris*, *Filago germanica*, *Urtica dioica*, *Phaseolus coccineus*, *Carlina vulgaris*. It may be that this globe-trotting butterfly has an even wider range of foodplants in Great Britain than is suspected.

**Dicker, G. H. L. (1944).** '*Tachyporus* (Col., Staphylinidae) larvae preying on aphides.' *Ent. Mon. Mag.* 80: 71.

In the peak period, 1943, there were from 30,000 to 50,000 beetle larvae per acre in the Wisbech area, but the strawberry aphid on which they fed was 500 times as numerous and they made little impression on it.

**Daltry, H. W. (1944).** 'Insects normally attached to Scrophulariaceae, feeding on *Buddleja*.' *Ent. Mon. Mag.* 80: 42.

The weevil *Cionus scrophulariae* on *Buddleja globosa*.

**Niblett, M. (1944).** 'British gall-causing Cynipidae. III.' *Entomologist*, 77: 84-9.

Records of *Biorhiza pallida*, *Andricus ostreus*, *A. furunculus*, *A. sieboldi*, *A. corticis*, *A. radialis*, *Diplolepis divisa*, *D. verrucosa*, *D. disticha*, *D. longiventris*, *D. similis*, *D. folii*, *Isocolus rogenhoferi*, their hosts and parasites.

## 5. POPULATION STUDIES

**Foster, A. H. (1944).** 'The red squirrel in north-west Hertfordshire.' *Trans. Herts. Nat. Hist. Soc. Fld Cl.* 22: 52.

Six records from 1939 to 1944 within a ten-mile radius of Hitchin, particularly in the wooded district to the south.

**Fordham, W. H. (1944).** 'Melanic grey squirrels in Hertfordshire.' *Trans. Herts. Nat. Hist. Soc. Fld Cl.* 22: 53.

Three records, two at one site; and an editorial suggestion that the black form is on the increase.

**Fisher, J. & Vevers, H. G. (1944).** 'The breeding distribution, history and population of the North Atlantic gannet (*Sula bassana*). Part 2. The changes in the world numbers of the gannet in a century.' *J. Anim. Ecol.* 13: 49-62.

In 1843 the world population of gannets was about 334,000 breeding individuals of which approximately two-thirds were on the Bird Rocks in the Gulf of St Lawrence. It decreased to about 106,000 in 1894 owing to depredations of man at the Bird Rocks, and since then has steadily increased to  $165,600 \pm 9,500$  in 1939, with the establishment of at least 9, probably 10 or 11, new colonies, some now large. The recovery was dominated by the recovery in south-west Britain. Now most of the 22 breeding colonies are protected. When small numbers are present, breeding is abnormally inefficient.

**Davis, H. H. & Tetley, H. (1944).** 'Studies on the biology of the Bristol Channel. XV. The Severn geese.' *Proc. Bristol Nat. Soc. for 1943*, 9: 494-509.

A valuable summary of available information on records, numbers and feeding grounds with notes on the probable migration routes. The two common species are white-fronted (*Anser albifrons*) and pink-footed (*Anser brachyrhynchus*).

**Alexander, W. B. (1944).** 'The index of heron population, 1943.' *Brit. Birds*, 37: 205-6.

The population, judged by sample counts, increased in England, Wales and Ireland by 14% since 1942. The increase was most marked in Ireland, the Midlands and south-west England.

**Johnston, T. L., Blezard, E. & Ellison, N. F. (1943).** 'Pied wagtail roost near Carlisle.' *Northw. Nat.* 18: 206-7.

Roost in September 1943 of about 700 pied wagtails (*Motacilla alba yarrellii*) in dense *Salix* bed on a river bank. The roost has been known for 30 years.

**Graham, M. (1943).** 'The fish gate.' London. Pp. 1-196.

This is an account of the marine fishing industry with particular emphasis on its human aspects. The various kinds of fishing are described, together with their history and economics. There is a general biological account, a history of the fishery investigations and a statement of the modern ideas about the best utilization of the stocks.

**Went, A. E. J. (1944).** 'Sea trout of the Waterville (Currane) River.' *Sci. Proc. R. Dublin Soc.* 23: 201-13.

It was found that the calculated smolt length of both the spring- and later-running sea trout was 3-4 in. greater than that of smolts from other Irish waters. Some of the large fry were being fished in mistake for small adult sea trout.

**Gross, F., Rayment, J. E. G., Marshall, S. M. & Orr, A. P. (1944).** 'A fish-farming experiment in a sea loch.' *Nature, Lond.* 153: 483-5.

Sodium nitrate and superphosphate added to Loch Craiglin, Argyll, was utilized within about four days. The most marked effect was on the  $\mu$ -flagellates, but the whole loch became one of the richest known plankton areas. The bottom fauna also increased considerably and marked fish showed rapid growth: flounders completed a normal 5-6 years of growth in less than two years. The low productivity of the sea compared with the land thus seems to be due to the shortage of plant nutrients.

- Hutton, J. A. (1944).** Wye Salmon, 1943: Report of the Wye Board of Conservators. Salm. Trout Mag. Lond. No. 111: 165-80.

The total catch of the Wye in 1943 was 2969 fish weighing 47,413½ lb. This was nearly the same as in 1942 and considering the reduced fishing effort during the war, is held to indicate a good crop. Details of the catches by various instruments and of the year-classes present are given, but owing to the war the statistics are not comparable with previous years. (See also Wye Board of Conservators, Annual Reports, in Section 7.)

- Hutton, J. A. (1944).** 'Salmon harvests: how runs may be forecast in Wye.' Salm. Trout Mag. Lond. No. 110: 40-64.

A review of the life history of the salmon and its application to forecasting the crop in future years. The crop is not related to the spawning seasons from which it is revived, but the number of a given year-class is apparently proportional to the number of the same year-class entering the fishing in earlier years.

- Ripper, W. E. (1944).** 'Biological control as a supplement to chemical control of insect pests.' Nature, Lond. 153: 448-52.

Within 3-30 years from the start of control, seven species of injurious insects in various countries have developed populations of mutants resistant to insecticides. Thus, while satisfactory control of the codlin moth in Colorado was achieved in two sprayings in 1900, twelve treatments were needed in 1930. Attention has therefore been given to developing chemicals that will destroy the pest and leave its parasites and predators unharmed. These clean up the survivors and so prevent the establishment of mutants. Success has been achieved with the cabbage aphid: nicotine vapour destroys 80-99% of the aphids and the rest are completely eliminated by several predators and one parasite. Fifty days after one treatment the experimental field was reinfested and at a higher density than the control field, since the beneficial insects had eventually starved to death. However, these aphids were not resistant mutants.

- Crombie, A. C. (1943).** 'The effect of crowding on the natality of grain-infesting insects.' Proc. Zool. Soc. Lond. A, 113: 77-98.

The survival rate of eggs and young larvae of *Tribolium* and *Oryzaephilus* was studied under different conditions of density. Although it was found that a high density interfered with oviposition, by far the most important effect was through the predatory habits of the adults and larvae. The rate of egg-eating increased immediately with an increase in density and fell similarly with a decrease. The effects were differential, because *Tribolium* preyed upon *Oryzaephilus* but not *vice versa*.

- Salt, G. & Hollick, F. S. J. (1944).** 'Studies of wireworm populations. I. A census of wireworms in pasture.' Ann. Appl. Biol. 31: 52-64.

A method by which complete wireworm populations can be collected from soil samples. Populations range up to 10 millions per acre in the top 12 in. of soil. Small larvae most abundant, decreasing numbers of larger larvae and comparatively few of the very large larvae is the typical composition of wireworm populations under old grass at all seasons of the year and in several fields in different parts of the country.

- Roebuck, A. & Bray, S. P. V. (1944).** 'Notes on the abundance, life-history and a teratological specimen of *Hypnoidus riparius* F. (Col., Elateridae).' Ent. Mon. Mag. 80: 73.

The larvae (wireworms) of this species are abundant in the upland pastures of Derbyshire, both the siliceous grassland with *Nardus stricta* dominant and the calcareous grassland with *Festuca ovina* dominant. Their numbers increase considerably at altitudes of over 800 ft. The average number is 35,000 per acre in 103 fields examined. This forms an appreciable part, actually 14%, of the total wireworm population. The largest number of *Hypnoidus* larvae in any one field has been 394,000 per acre. From rearing tests it seems clear that larvae are only found in the last two instars. The real populations are, therefore, considerably higher.

- Pearce, E. J. (1944).** '*Brachygluta* (= *Bryaxis*) *haematica* Reich (Col., Pselaphidae) in South Devon.' Ent. Mon. Mag. 80: 71.

Notes localization of a species to a very restricted area. A hundred specimens could have been obtained in an old earthy stump, and a few were found in three other places nearby, but many apparently suitable habitats yielded none.

- Beirne, B. P. (1944).** 'The causes of the occasional abundance or scarcity of wasps (*Vespula* spp.) (Hym., Vespidae).' Ent. Mon. Mag. 80: 121-4.

Between 1864 and 1931 there were ten seasons in which wasps were exceptionally abundant throughout England and Wales in the summer and autumn: 1864, 1880, 1883, 1887, 1890, 1893, 1902, 1911, 1919, and 1921. There were ten seasons in which they were exceptionally scarce: 1865, 1879, 1886, 1894, 1897, 1903, 1910, 1918,

1920 and 1924. Although the seasons of abundance or of scarcity occurred on an average of every seven years, there was no apparent periodicity. Their abundance appears to be irrespective of the abundance of the queens in the spring. In seasons of wasp abundance the rainfall during April, May and June was low, while in seasons of scarcity it was high. Seasons of abundance and scarcity usually occur in pairs. It is possible that, in seasons of wasp scarcity, disease, which often destroys a large proportion of the larvae, becomes correspondingly scarce, and as it does not increase at the same rate as the wasps they become relatively abundant in the following year, while in seasons of wasp scarcity the reverse takes place.

**Benson, R. B. (1944).** 'Swarming flight of *Blacus tripudians* Haliday (Hym., Braconidae).' Ent. Mon. Mag. 80: 21.

An enormous swarm hovering in the air like gnats, concentrated at a height of from about 6-10 ft. above the road.

**Donisthorpe, H. (1944).** 'The dancing habits of some Braconidae (Hym.).' Ent. Mon. Mag. 80: 72.

All individuals caught in a dancing swarm were males.

**de Worms, C. G. M. (1944).** 'Prevalence of *Rhyacia simulans* in the Salisbury district.' Entomologist, 77: 27.

1943 was a remarkable year for this usually scarce and local moth, first reported in the Salisbury district in 1941. It has been taken in many localities where it had not been previously noted, while in the Cotswolds it was seen in great abundance during the latter half of June.

**Harrison, J. W. Heslop (1944).** 'Abundance of *Tethea or* in the Isles of South Uist (Outer Hebrides) and in the Isle of Rhum (Inner Hebrides).' Entomologist, 77: 12.

Colossal numbers of larvae of this moth were noted in the Hebrides in 1943. The climax was reached on Rhum on aspens in a gorge in the east of the island where on one tree alone there must have been five or six thousand larvae, and other trees were only a little less productive.

**Fletcher, T. Bainbrigge (1944).** 'Longevity of *Epipsilia (Rhyacia) simulans*.' Ent. Rec. 56: 9-10.

A female specimen of this Agrotid moth lived in captivity at least three, perhaps four months.

**Barker, A. N. (1943).** 'Biological assay in sewage purification.' Proc. Leeds Phil. Lit. Soc. 4: 87-96.

Techniques for sampling populations of Protozoa.

## 6. MIGRATION, DISPERSAL AND INTRODUCTIONS

**Lack, D. (1943-4).** 'The problem of partial migration.' Brit. Birds, 37: 122-30, 143-50.

In general, British 'resident' species either show a southward dispersal in winter, or migrate partially, individuals either staying on their breeding grounds or making a considerable journey. In addition birds from England often winter in south-west Europe, while Scottish birds move to Ireland; further complication is added by females and juveniles of some species migrating in greater numbers than males. Thus some resident populations are polymorphic in winter behaviour.

**Tetley, H. (1944).** 'Regularity in migration of swifts.' Proc. Bristol Nat. Soc. for 1943, 9: 481-2.

Records of arrival and departure from one nesting site from 1935 to 1943. Arrival dates varied between 3 and 12 May, departures between 5 and 14 August, length of stay between 89 and 96 days.

**Allen, K. R. (1944).** 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 4. The smolt migration in the Thurso River in 1938.' J. Anim. Ecol. 13: 63-85.

In this study, based on counts and measurements at four traps, activity declined after measurements began, then increased to a maximum during which practically all smolts left the upper part of the river-shoals. Waves of migration move slowly down the river. Observed rates, determined by marked fish, range from 0.1 to 6 km. per day. Rises in water level appear to act as stimuli. Temperature also probably has an effect, though much smaller, and passing of actively migrating smolt also seems to act as a stimulus. The great majority of smolts migrated after 2 years. Spring growth makes size at migration more uniform than at the end of winter. There is an apparent relation between size and readiness to migrate. The average rate of smolt development, determined from the colour of the pectoral fins, was about 0.08 per day on a scale in which 4 represents full development. Smolt development is associated with a slight decrease in condition.

**Dannreuther, T. (1944).** 'Migration records, 1943.' *Entomologist*, 77: 55-60, 73-7.

In 1943 insect immigration was generally above the normal in scale and exceptional in the unprecedented invasion of the striped hawk-moth (*Celerio lineata livornica*), which spread all over the British Isles. In Cornwall alone it exceeded all previous records in abundance. *Acrolepia assectella*, a microlepidopteron new to Britain, was found attacking leeks in Sussex. A general summary and notes on abundance, distribution, and movements of scheduled species are given.

**Dannreuther, T. (1943).** 'The striped hawk-moth record immigration of 1943.' *S. East. Nat.* 48: 56-8.

Large migration of *Celerio lineata livornica*. 159 specimens were captured and 500 county records made, mostly from south-west counties; one was captured at Aberdeen. 31 wild larvae were found in July.

**Adkin, G. T. (1944).** 'The 1943 invasion of *Celerio lineata livornica* Esp. in Cornwall.' *Entomologist*, 77: 33-8.

About 500 adults of the striped hawk-moth were seen in the British Isles in 1943, 280 of them in Cornwall.

**Jary, S. G. & Edelsten, H. M. (1944).** '*Acrolepia assectella* Zell. (Lep., Plutellidae) in England.' *Ent. Mon. Mag.* 80: 14-15.

Larvae of this moth are reported causing damage to leeks at Bexhill. It is presumed that the insect has migrated from the Continent.

**Turner, A. D. (1944).** '*Papilio machaon* in Surrey.' *Entomologist*, 77: 21.

A specimen of the swallow-tail seen on the North Downs between Dorking and Guildford, 15 August 1943.

**Beirne, B. P. (1944).** 'The origin of the maritime Lepidoptera of Lough Neagh.' *Irish Nat. J.* 8: 167-71.

*Agrotis vestigialis*, *A. tritici*, *Procus literosa*, *Euzoa nigricans*, *Stilbia anomala* and *Epirrhoë galiata* are all species which have otherwise exclusive or almost exclusive maritime distribution. Concludes that these species probably migrated along a direct connexion between Lough Neagh and the sea in the early Post-Glacial period.

**Walker, J. (1944).** 'On the drift of the Jersey tiger moth: *Callimorpha quadripunctaria* (hera).' *Trans. Torquay Nat. Hist. Soc.* for 1942-3, 9: 19-22.

Indicates a spread from a limited area around Dawlish in 1901, south to Torquay and Brixham and north across the mouth of the river Exe by 1942. This species seems to prefer built-up areas.

**Fisher, R. C. (1944).** 'A note on *Paratillus carus* Newm. (Col., Cleridae) and records of its occurrence in Great Britain.' *Ent. Mon. Mag.* 80: 132-4.

This Australian insect is a common predator of *Lyctus* powder-post beetles. Its probable acclimatization and establishment in this country, together with its continued importation in *Lyctus*-infested woods from Australia, may ultimately lead to it becoming as frequently associated with *Lyctus* in the United Kingdom as the related Clerid, *Tarsostenus univittatus* Rossi.

**Lloyd, R. W. (1944).** 'Occurrences of *Syagrus intrudens* Waterh. (Col., Curculionidae) in Britain confirmed.' *Ent. Mon. Mag.* 80: 4.

This fern-weevil belongs to a genus otherwise exclusively Australian. It was described from the Botanical Gardens, Dublin, in 1903 and found in Sussex in 1932. In 1943 it occurred in both these localities, but so far it has not yet been found in Australia.

**Gimingham, C. T. & Gimingham, C. H. (1944).** 'Further notes on *Clypeoaphis suaedae* Soliman (Hem., Aphididae).' *Ent. Mon. Mag.* 80: 25-7.

This Egyptian species feeding on *Suaeda vera* was recently reported in Britain on *S. maritima*. In addition to the original locality in Cornwall it is reported from north Devon and Norfolk. Sexual forms previously unknown are described.

**Kevan, D. K. McE. (1943).** 'Study of an introduced North American freshwater mollusc, *Stagnicola catascopium* (Say).' *Proc. R. Phys. Soc. Edinb.* 61: 430-61.

The snails, introduced on logs from eastern Canada, breed in a warm engine pond 72 x 36 x c. 7 ft. deep. There was a gradual decrease in density from top to bottom of the walls (105 down to 36 snails per sq. ft.)

probably correlated with decreasing supply of non-cellular algae. Altogether there were about a quarter of a million snails. There was a heavy mortality of about 96% in the second of the two main broods, probably due to great overcrowding, but good survival in the brood produced after the annual cleaning of the pond. The shell shows great variation.

#### 7. REPORTS OF ORGANIZATIONS

**Freshwater Biological Association of the British Empire (1944).** Twelfth Annual Report for the year ending 31st March, 1944. 37 pp. Price to non-members, 1s. 6d. (F.W.B.A., Wray Castle, Ambleside, Westmorland.)

Besides an account of the administration of the laboratories at Wray Castle the Report includes non-technical accounts of the scientific work in progress: on the habits and life history of eels, on the effect of drastic reduction of the perch population of Lake Windermere, on seasonal variations in algae and on lake deposits and sedimentation.

**Wye Board of Conservators.** Annual Reports: Season 1940, 11 pp.; 1941, 10 pp.; 1942, 10 pp.; 1943, 10 pp.

Contains annual statistics of the numbers and weights of salmon, with weight-group analyses of large samples, and field observations on the annual runs and spawning conditions. There was little salmon disease during this period. The salmon population seems to have been well maintained, netting being on a much reduced scale, but rod-fishing on some large stretches giving good catches. General notes also on trout, coarse fish, experiments on trapping eels, and on vigilant protection of the river system from pollution. The 1941 Report has an interesting estimate of the total fish caught in the Wye system, as a contribution towards food supply, based on salmon catches (e.g. c. 25 tons in 1941, c. 75 tons in 1936), sample trout and grayling catches (e.g. 3 cwt. on 3 miles of river), impressions of the results of coarse fishing backed by actual sample figures from one large angling association (e.g. nearly a ton of pike in 1938). The final estimate, admittedly very rough, is (allowing a guess of 20 tons of coarse fish) 65-100 tons altogether, and possibly more in a very good salmon season.

**Eire, Department of Agriculture, Fisheries Branch (1943).** 'Report of the Minister for Agriculture on the sea and inland fisheries for the year 1942.' Dublin, 24 pp. Price 6d.

5000 young oysters were obtained in preliminary breeding experiments. The output from two brown trout hatcheries was over a million ova and 35 'hatching out' stations were operated. An investigation of the food of the pike has started. There are 16 appendices.

**Yorkshire Fishery District (1944).** Seventy-seventh Annual Report on the Salmon, Trout, and Freshwater Fisheries in Yorkshire (1943) (by R. W. Ward). York. 28 pp.

Salmon catches were very low in the river. In the estuary (of the Ouse) they were higher than in the two previous years. Abnormal war-time conditions of labour and the rivers make the changes difficult to interpret. The number of migratory trout, all taken in the sea, was the lowest since 1890. River trout fishing was quite good. 1000 grayling were transferred from one area to another. Kield Head Hatchery for trout proved difficult to manage owing to water shortage, and plans have been made to transfer hatchery activity to High Costa Mill at Pickering. Since its start in 1932 Kield Head Hatchery reared and distributed £5981 worth of trout. In spite of new war industries, little serious river pollution has occurred. An increase of bream (*Abramis brama*) is reported in the river catches of anglers in recent years.

**Lancashire and Cheshire Fauna Committee (1944).** Twenty-sixth Report and Report of the Recorders for 1939-42. Part 1. 36 pp.

Lists, often with habitat and other data. Mammals (coypu on the Ribble), birds (H. W. Robinson); non-marine Mollusca (J. Wilfrid Jackson); marine Amphipoda (W. M. Tattersall); Lepidoptera (W. Mansbridge) sawflies (H. W. Miles); dragonflies (W. K. Ford); Parasitic Hymenoptera (G. J. Kerrieh).







